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Programa de Pós-Graduação em Ecologia e Evolução

CARLOS EDUARDO KLEIN DE OLIVEIRA

Modelos Mecanicistas Para Entender Dinâmicas Populacionais e Adaptação Termal Como Fatores Emergentes

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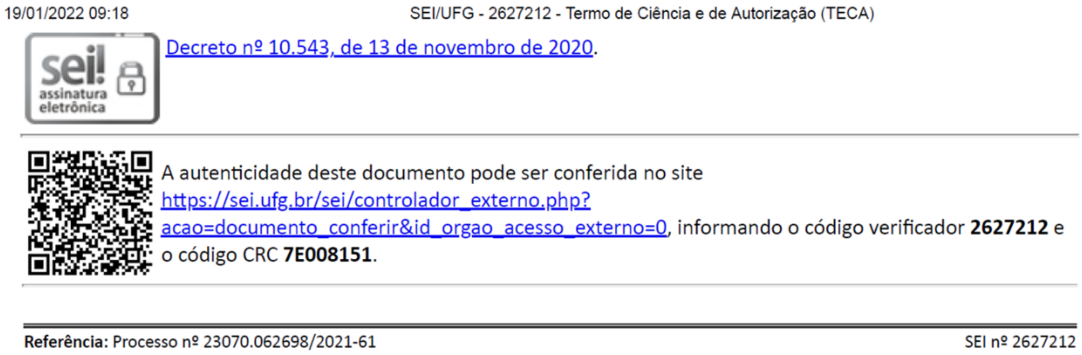

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CARLOS EDUARDO KLEIN DE OLIVEIRA

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Tese apresentada ao programa de Pós-Graduação em Ecologia e Evolução, do Instituto de Ciências Biológicas da Universidade Federal de Goás, como requisito para obtenção de título de Doutor em Ecologia e Evolução.
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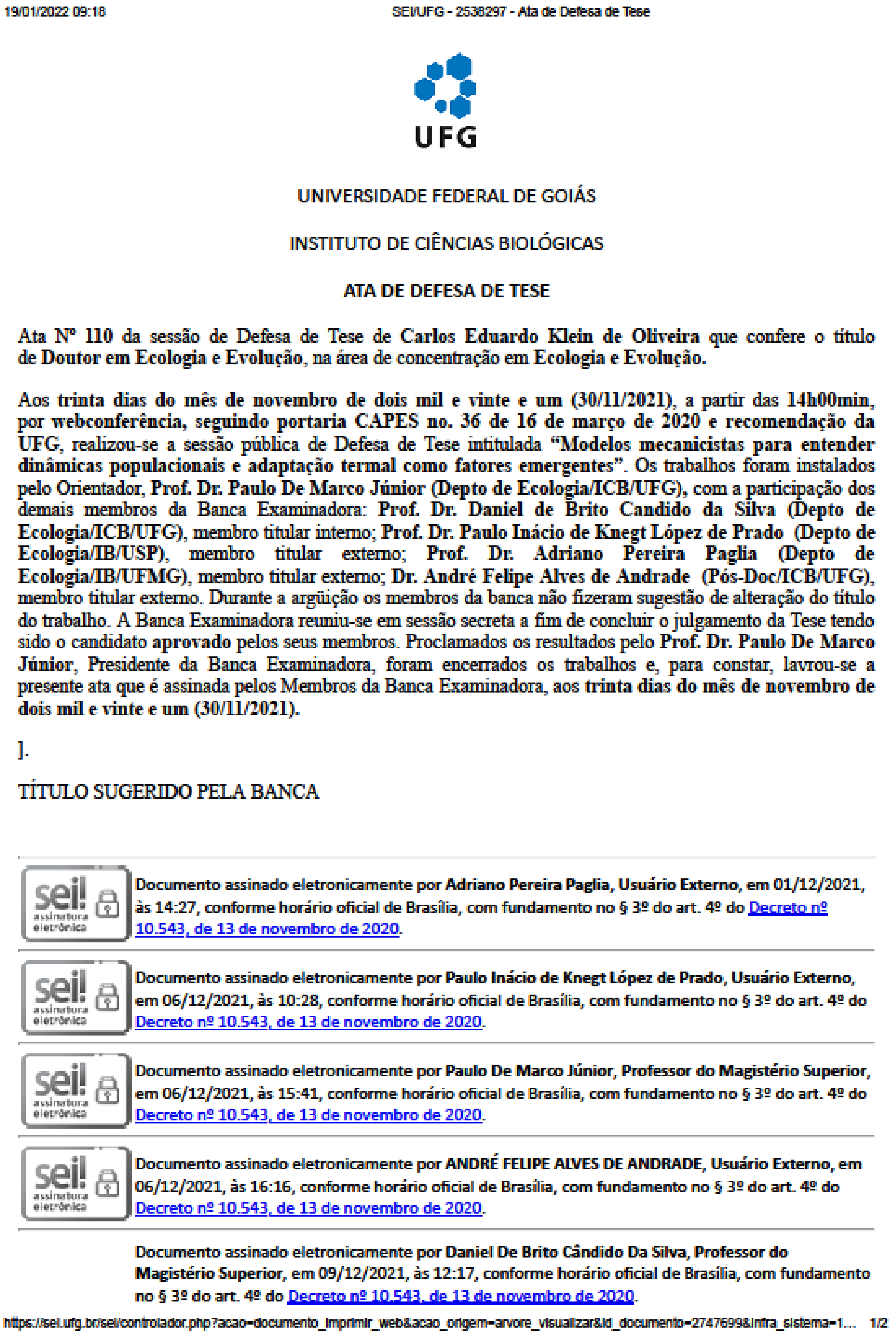

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Ata Nº 110 da sessão de Defesa de Tese de **Carlos Eduardo Klein de Oliveira** que confere o título de **Doutor em Ecologia e Evolução**, na área de concentração em **Ecologia e Evolução.**

Aos **trinta dias do mês de novembro de dois mil e vinte e um (30/11/2021)**, a partir das **14h00min**, **por webconferência, seguindo portaria CAPES no. 36 de 16 de março de 2020 e recomendação da** UFG, realizou-se a sessão pública de Defesa de Tese intitulada **"Modelos mecanicistas para entender dinâmicas populacionais e adaptação termal como fatores emergentes"**. Os trabalhos foram instalados pelo Orientador, **Prof. Dr. Paulo De Marco Júnior (Depto de Ecologia/ICB/UFG)**, com a participação dos demais membros da Banca Examinadora: **Prof. Dr. Daniel de Brito Candido da Silva (Depto de Ecologia/ICB/UFG)**, membro titular interno; **Prof. Dr. Paulo Inácio de Knegt López de Prado (Depto de Ecologia/IB/USP)**, membro titular externo; **Prof. Dr. Adriano Pereira Paglia (Depto de Ecologia/IB/UFMG)**, membro titular externo; **Dr. André Felipe Alves de Andrade (Pós-Doc/ICB/UFG)**, membro titular externo. Durante a argüição os membros da banca não fizeram sugestão de alteração do título do trabalho. A Banca Examinadora reuniu-se em sessão secreta a fim de concluir o julgamento da Tese tendo sido o candidato **aprovado** pelos seus membros. Proclamados os resultados pelo **Prof. Dr. Paulo De Marco Júnior**, Presidente da Banca Examinadora, foram encerrados os trabalhos e, para constar, lavrou-se a presente ata que é assinada pelos Membros da Banca Examinadora, aos **trinta dias do mês de novembro de dois mil e vinte e um (30/11/2021).**

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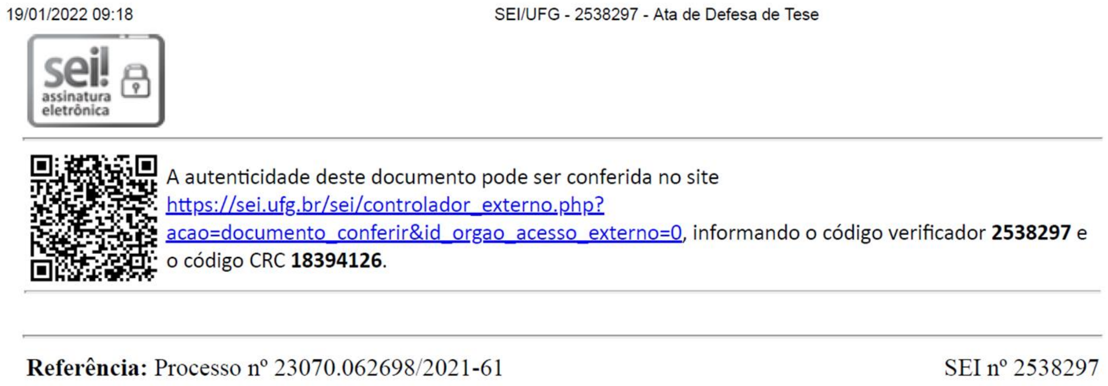

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SUMÁRIO

RESUMO GERAL

Primeiramente, no primeiro capítulo, apresentamos uma revisão sobre os efeitos da temperatura em organismos e níveis de organização superiores. No segundo capítulo, o objetivo foi de desenvolver um IBM realista em relação a interação de dinâmica populacional e regimes de flutuação de temperatura, que consiga ser geral o suficiente para ser aplicado a várias espécies. Nesse capítulo, usamos os avanços da ecologia termal apresentados no primeiro capítulo, acoplado a alguns princípios da teoria de orçamentos energéticos dinâmicos (teoria DEB) para obter resultados populacionais realistas e bem embasados para espécies virtuais geradas aleatoriamente. No terceiro capítulo, aplicamos o modelo desenvolvido a um cenário de mudança ambiental, incorporando variabilidade e herdabilidade nos traços, para assim simular adaptação rápida de maneira emergente, e consequentemente, gerar avanços teóricos para o sistema explorado.

Palavras-chave: Modelo Baseado em Indivíduo, dinâmica populacional, temperatura, adaptação termal, ecologia termal.

GENERAL ABSTRACT

At first, I review the effects of temperature on organisms and higher levels of biological organization in the first chapter. After that, in the second chapter, my goal was to develop an IBM that predicts realistic population dynamics in different temperature regimes, and that can be general enough to account for the responses of a variety of species. I used theoretical knowledge of thermal ecology, coupled with some principles of dynamic energy budget theory to reach realistic population outcomes for generated random species. After those models were complete, in the third chapter, I incorporated variability and heritability in the organisms' thermal traits, so that it was be possible to glimpse on the possibilities for fast adaptation to abrupt changes in temperature. A mechanistic approach to those questions can be important for theoretical developments, and may open possibilities to understanding of other questions related to models' assumptions and predictions.

Keywords: Individual based model, population dynamics, temperature, thermal adaptation, thermal ecology.

INTRODUÇÃO GERAL

Modelos matemáticos são muito usados nas ciências biológicas, tanto em questões de caráter teórico como práticos. Ao longo do tempo, os avanços tecnológicos ligados à computação e as mudanças nos paradigmas na ecologia causaram mudanças na maneira como construímos modelos e exploramos teorias. Uma importante inovação com relação a modelos matemáticos foi o surgimento dos modelos baseados em indivíduo (IBMs). Essa nova abordagem representa uma nova oportunidade de colocar em modelos alguns processos ou aspectos normalmente não utilizados nos modelos mais clássicos, como por exemplo variação individual e interações detalhadas entre indivíduos (Judson 1994; Grimm 1999). Além disso, os IBMs proporcionam maior mecanicismo nos modelos, já que eles inferem padrões nas populações ou comunidades que emergem do funcionamento dos indivíduos. Modelos considerados mecanicistas são os que usam processos biológicos de maneira explícita, e por isso esperamos que sejam melhores ao extrapolar resultados para condições desconhecidas (Buckley *et al.* 2010; Denny & Benedetti-Cecchi 2011). Os IBMs têm sido uma ferramenta muito usada na ecologia e em outras áreas da ciência como as ciências sociais, economia, geografia, ciências políticas dentre outras (Grimm *et al.* 2006).

O impacto humano nos sistemas biológicos, como a poluição, a fragmentação de ambientes e mudanças climáticas, cria a necessidade de predições precisas e realistas a respeito de como as espécies podem responder a essas pressões. Dois dos possíveis resultados causados por mudanças no clima são: 1) as espécies se movem, rastreando condições melhores para suas populações e 2) as populações ficam onde estão, e se adaptam ao novo clima. Sendo assim, uma análise eficiente dos efeitos de mudanças climáticas deve considerar as dinâmicas e os potenciais adaptativos e evolucionários das espécies (Kearney *et al.* 2009; Atkins & Travis 2010; Bridle *et al.* 2010). Existem evidências de adaptação fisiológica local em várias espécies (Atkins & Travis 2010), um exemplo delas é sobre o efeito da temperatura no desenvolvimento de Aedes e como essa relação muda geograficamente (Kearney & Porter 2009). Existem publicações atuais reafirmando a importância de tratar a fisiologia evolutivamente (Chown *et al.* 2010), que mostram que esses processos podem ser mais importantes do que consideramos no momento (Luo & Koelle 2013), e outros que mostram exemplos de evolução rápida empiricamente, relacionados por exemplo com resistência a toxinas e a invasões biológicas (Chown *et al.* 2010). Modelos ecofisiológicos deveriam idealmente ser parametrizados com um grande número de diferentes populações distribuídas ao longo da ocupação da espécie (Kearney *et al.* 2009). Isso evitaria que a micro- adaptação de populações enviesasse o resultado geral. Essa quantidade de informação nem sempre está disponível para todas as espécies, e por isso outra opção é incorporar variação nos traços (adaptação) nos modelos. Até o momento, entretanto, os estudos que avaliam ou preveem os impactos de mudanças climáticas nas espécies têm focado pouco nas questões relacionadas ao efeito da adaptação das espécies em suas distribuições (Atkins & Travis, 2010), e poucos estudos têm adotado abordagens evolutivas para o problema, no geral (Buckley *et al.* 2010; Leroux *et al.* 2013).

Os estudos que usam modelos para entender a adaptação da ecofisiologia das espécies e a relação disso com os seus ranges são em sua grande maioria modelos de variáveis-estado, que usam relações entre o fitness de populações e gradientes ambientais para criar suas predições (Burger & Lynch 1995; Kirkpatrick & Barton 1997). Esses modelos constroem uma fundação teórica forte acerca das dinâmicas de distribuições de espécies e adaptação local. Esses modelos, porém, ignoram efeitos complexos que podem afetar os sistemas como por exemplo a dinâmica populacional, as histórias de vida das espécies e os mecanismos básicos pelos quais o ambiente influencia o fitness dos indivíduos. A nossa proposta é criar teoria relacionada à adaptação fisiológica pensando o fitness dos indivíduos como uma característica emergente em relação à dinâmica populacional e à eco-fisiologia dos organismos, em um IBM. A maneira como a história de vida e a eco-fisiologia dos indivíduos se relacionam com o ambiente, em um modelo geneticamente explícito, pode gerar resultados contra-intuitivos, além de possivelmente criar hipóteses ecológicas a serem testadas. O objetivo dessa tese é desenvolver um modelo de dinâmica populacional baseado em indivíduo, simulando mecanisticamente os efeitos da temperatura, levando em conta fatores demográficos e variação intra-específica em traços explicitamente. A maneira pela qual a história de vida dos organismos e sua eco-fisiologia poderia interagir com a dinâmica populacional e o ambiente, em um IBM, pode levar a resultados interessantes acerca de padrões macro ecológicos, e esse avanço teórico poderia ser útil para avançar acerca das limitações de modelos de distribuição e predições sobre os efeitos de mudanças climáticas.

Primeiramente, no primeiro capítulo, apresentamos uma revisão sobre os efeitos da temperatura em organismos e níveis de organização superiores. No segundo capítulo, o objetivo é de desenvolver um IBM realista em relação a interação de dinâmica populacional e regimes de flutuação de temperatura, que consiga ser geral o suficiente para ser aplicado a várias espécies. Nesse capítulo, usamos os avanços da ecologia termal apresentados no primeiro capítulo, acoplado a alguns princípios da teoria de orçamentos energéticos dinâmicos (teoria DEB, van der Meer 2006; Kooijman 2010) para obter resultados populacionais realistas e bem embasados para espécies virtuais geradas aleatoriamente. No terceiro capítulo, aplicaremos o modelo desenvolvido a um cenário de mudança ambiental, incorporando variabilidade e herdabilidade nos traços, para assim simular adaptação rápida de maneira emergente, e consequentemente, gerar avanços teóricos para o sistema explorado.

CHAPTER 1 – CONCEPTS, ADVANCES AND CHALLENGES IN THERMAL ECOLOGY

Abstract

Thermal ecology is the field that investigates the effects of temperature on biochemical reactions, enzyme functioning, performance and preference of organisms and its' consequences on higher ecological organization. The field has strong theoretical basis, in the form of the classical thermoregulation and optimality models, which theorize on how much the individuals should thermoregulate and how thermal performance and tolerance may be driven by environmental temperature variability. The field has a very experimental oriented approach, displaying a variety of experimental and empirical approaches to its' questions, including rearing and preferred temperature experiments, but also selection and breeding experiments. Observational studies are also performed. Thermal ecology has been successful both in understanding species differences and specificities and in escalating to higher hierarchical levels (community and macroecological). I argue that the most important challenges to the field are relative to the validation and unification of its' basal theory and in possible applications to help forecasting the effects of climate change.

Keywords: Temperature, Thermal Ecology, Sensitivity, Preference, Thermoregulation.

Introduction

The relationship between organisms and their environments is basal for ecology, and temperature is probably the most important abiotic factor, affecting species in various levels (physiological, behavioral, populational and evolutive). The pervasive importance of this single factor justifies raising its study to the level of a relevant subdiscipline – Thermal Ecology (hereafter TE) – with specific objects and theoretical structure. At first, temperature affects the organism's chemical reactions. This happens through many factors like the proteins' stability and flexibility, the fluids' viscosity and freezing possibility, the dynamics of solutes and membranes and diffusion processes, among others which are dependent on temperature (Clarke 1991; Somero 1995; Somero *et al.* 1996; Fields 2011). Among those factors, the effect of temperature on proteins activity and stability is probably the most important (Somero 1995; Fields 2001). Proteins' activities are responsible for a plethora of biological processes, from cell division and growth to digestion and muscle contractions, among a large number of others. Proteins are usually enablers of specific chemical reactions, which may be anabolic (production of more complex compounds, associated to growth and reproduction) or catabolic (breaking complex compounds into lower parts, associated with digestion and respiration). In order to enable some reaction, a protein must have the accurate physical conformation to bind to the other reagent molecules, and binding to other molecules is a process highly dependent on kinetic energy (Somero *et al.* 1996). The effect of temperature on proteins is dependent on the need to reach an energy threshold called activation energy to enable reactions (Somero 1995; Somero *et al.* 1996). An environment with a relatively high temperature thus will make the fitting of proteins to their substrates very frequent, making reactions more efficient, although it may also lead to changes in the proteins' physical structure so that it cannot fit reagents anymore and is thus called denaturized. Environments with lower kinetic energy, or relatively cold, will cause the frequency of reactions to be lower, and proteins frequently will not reach their activation energy thresholds (Fields 2001). Environments with high kinetic energy cause high frequency of reactions and therefore higher metabolism, but also pose more risks due to protein denaturation.

The functioning of multiple proteins, through anabolic and catabolic processes and chemical pathways (the metabolism), affect organisms' physiology impacting processes such as locomotion and sensing capabilities, growth and development rates and the maintenance of homeostasis and life (Bayard H. Brattstrom 1963; Clarke 2003; Chaui-Berlinck *et al.* 2004). Temperature has been acknowledged to affect organisms' cell cycle duration, respiration rates, basal and standard metabolic rates, heart rates, locomotion speed, migration potential, melanism, growth and developmental rates, fecundity rates among many others (Bogert 1949; Bullock 1955; Brett 1971; Dawson 1975; Harper *et al.* 2000; Brodeur *et al.* 2003; Clarke & Fraser 2004; Bowler & Terblanche 2008; Hoefnagel & Verberk 2015; Walczyńska *et al.* 2015; Gaitán-Espitia *et al.* 2017; Hassanalian *et al.* 2017; Hu *et al.* 2019). This impact is usually seen as phenotypic plasticity: a set of different performances or characteristics, expressed by a single genotype, dependent and regulated by the environment. At higher organization level, temperature ends up affecting species' population dynamics and occurrence, through changing organisms' reproduction, survival, the efficiency of assimilation of resources and the speed of life history processes and overall phenology (Walker *et al.* 2015; Mccardle & Fontenot 2016; Cherkiss *et al.* 2020). In the evolutionary scale, it may also affect speciation, extinction and mutation rates (Rohde 2013; Gillman & Wright 2014). Because of this, there has been interest in the usage of thermal ecology as a tool for understanding species ranges (Walker *et al.* 2015), the potential to invasion of new areas (Litmer & Murray 2019), predicting the impacts of climate change (Helmuth *et al.* 2005; Chown *et al.* 2009; Kearney & Porter 2009; Angert *et al.* 2011; Gvoždík 2018; Terblanche & Hoffmann 2020) and also to management of livestock (Ibrahim & Quick 1994) and in public health issues (Yang *et al.* 2009, 2011; Padmanabha *et al.* 2012).

When individuals are exposed to harsh temperatures, they have a variable set of possible behavioral and physiological responses or compensations. The first and fast option for a species is thermoregulation. In larger time scale, organisms may adjust their physiologies and get acclimated, hardened or enter torpor. These responses may correlate to each other and become adaptive depending on the environment (daily and annual temperature fluctuation, temperature predictability in different seasons) (Beck 1977; Nilsson-Örtman *et al.* 2012; Bartheld *et al.* 2017), the species life history (the seasons when important life history processes occur) (Bowler & Terblanche 2008; Halliday & Blouin-Demers 2017) and interactions with other species (basking reptiles may be more prone to predation, hibernation may be related to the availability of prey) (Brett 1971; Sherman 2008; Kronfeld-Schor & Dayan 2013). Organisms developed various adaptations in order to deal with harsh environmental temperatures and its' variability. Cold-adapted organisms developed adaptations such as higher mitochondria quantity in muscles, different brain cell microtubules so that nervous conduction can work below 0°C, and proteins designed to avoid freezing of fluids (Clarke 1991; Somero *et al.* 1996). Species in hot environments developed adaptations such as Heat Shock proteins (Hoffmann *et al.* 2003), homolog enzymes (Fields 2001) among others. Temperature is a very variable factor (daily, seasonally and geographically) that is very often correlated to other abiotic and biotic environmental factors (e.g., precipitation and air humidity, oxygen availability and altitude, species richness and resources availability), and this makes its effects hard to assess. This "mechanistic cascade" of responses and correlations, in the words of Angilletta *et al.* (2006), makes of TE a very complex field in relation to its theories, experimental approaches and possible applications (Angilletta *et al.* 2006).

My objective here is to review the main concepts, advances and challenges in TE, separating between a theoretical and an empirical approach, and I will also discuss some possible applications in other areas of ecology. At first, I will review the most important theoretical advances relative to thermoregulation behavior, thermal sensitivity and the consequences of those for higher ecological organization levels (community and macroecological). After that discussion, I will review how scientists have empirically approached TE, showing what types of experiments are performed, the enhancements they underwent through time and the most interesting and general conclusions. After that, I conclude by discussing the challenges and unresolved questions in TE, proposing some interesting research paths and discussing its importance for facing climate change.

Theoretical Developments

In this section, I will briefly explore the theoretical foundations of TE and their impacts to higher organization levels (community and macroecological). The most important predictions of the theory, organized through hierarchical levels are summarized in table 1.

Table 1: A briefing for the theories, hypothesis and patterns that I will address in more detail through the section.

Hypothesis/Pattern and Organization level	Predictions/Explanations
Organism/Species	
Coadaptation Hypothesis (Huey & Slatkin 1976; Gilbert & Raworth 1996)	Species/Organism preferred temperature match optimum.
Suboptimality hypothesis (Martin & Huey 2008)	Species/Organism preferred temperature slightly lower than optimum
Thermodynamic Effect (Asbury & Angilletta 2010)	Species/Organism optimum temperature is slightly higher than optimum
Trait Variation Hypothesis (Haupt et al. 2017)	Preference matches optima only in traits important for fitness
Thermoregulation behavior (Huey & Slatkin 1976)	Thermoregulation behavior increases when: costs are low (high availability of ideal temperature sites); benefits are high (specialized species); environment is too harsh (environment much different from optimum);
Thermoregulation behavior (Vickers *et al.* 2011)	Hotter environments should lead to higher thermoregulation frequency;
"Jack of all temperatures is a master of none"	A species cannot display maximum performance in all temperatures.
"Hotter is better"	Organisms in hotter environments display higher fitness and performance. It is a consequence of the thermodynamic constraint.
Optimallity Theory (Lynch & Gabriel 1987)	Environmental variation within generations is stronger driver for tolerance breadth. Higher environmental variation causes broader, less specialized, Thermal Performance Curves.
Optimallity Theory (Gilchrist 1995)	Thermal specialists should overall be the rule. Thermal generalists should happen only when variation among generations is high.

Optimallity Theory (Huey & Kingsolver 1993)	If thermal tolerance breadth is consequence of genetic variation, thermal breadths above intermediary sizes are optimal for accommodating climate change
Community	
Predator-prey dynamics (O'Connor *et al.* 2011; Dell *et al.* 2014)	Temperature affects dynamic equilibrium of the system; Temperature changes may lead to extinction by overexploitation;
Predator-prey dynamics (Mitchell & Angilletta 2009)	Predator lethality influences prey habitat choice (thermoregulation) and specialization. Highly lethal predators should influence prey to be more generalist;
Invasion processes and phenology (Rudolf & Singh 2013; Grainger *et al.* 2018)	Priority effect is stronger in hotter environments;
Food webs (Petchey *et al.* 1999; Clarke 2003; Kordas *et al.* 2011)	Food webs in higher temperatures have less energy flowing through hierarchical levels; Global warming poses greater risks for top-chain predators and herbivores.
Macroecological	
Latitudinal Diversity Gradient (LDG) (Brown *et al.* 2004)	Higher mutation rates result of higher temperatures due to chemical damage on DNA.
LDG (Puurtinen *et al.* 2016)	Cold places jeopardize beneficial mutation because of cold-adapted proteins stability.
LDG (Clarke & Gaston 2006)	Higher speciation rates in warm latitudes because they are more amenable.
LDG (Stevens 1989)	Temporal variability leads to higher specialization and diversity.
Temperature-Size Rule (Berrigan & Charnov 1994; Walters & Hassall 2006)	Caused by discrepancies in the enthalpies and sensitivities for Growth and Development processes.
Temperature-Size Rule	Caused by steep fitness gains from larger size specifically at cold temperatures.
Metabolic cold adaptation (Wohlschlag 1964)	Cold-adapted species compensate temperature by increasing metabolism.

THERMAL PREFERENCE THEORY

The first theoretical developments on TE discussed approaches thermoregulation and thermal preference. Thermoregulation stands for the capacity of an individual to maintain its' body temperature different from environmental temperature, and thermal preference stands for the environmental temperature chosen by an organism when free to do so. The two concepts are related by the fact that one method for thermoregulating is by finding microhabitats that match the preferred temperature, such as cool underground holes or rocks heat by the sun. It was proposed, both verbally (Dawson 1975; Gilbert & Raworth 1996) and by mathematical models (Huey & Slatkin 1976) that 1) thermal preference should match the temperatures most experienced by the organisms in space and time, and 2) that preferences should also match the thermal sensitivity, or the optimum values for the species/organism. Those two patterns should happen because this correlation should enhance fitness. This proposition is called the coadaptation hypothesis, based on the idea that thermal preferences, thermoregulation capacities and the temperature optima adapt together.

There are interesting alternatives to the coadaptation hypotheses. Martin & Huey (2008) propose that thermal preferences will usually be slightly cooler than Optimal Temperatures. They are based on the assumptions that species are never perfect thermoregulators and that Thermal Performance Curves (discussed below) “punishes” overheating more than cooling because of their skewedness. This suboptimality should happen so that species can avoid the dangers of overheating, and this prediction was called the suboptimality hypothesis. Another proposition was made regarding the thermodynamic constraint (Asbury & Angilletta 2010). They made some changes on older optimality models in order to account for the constraint. The thermodynamic constraint poses that biological adaptation is not able to totally compensate for cold temperatures, which slows down chemical processes and causes performance and metabolism to always be more efficient and higher in hotter environments. The model of Asbury & Angilletta (2010) predicts that optimal temperatures should be higher than thermal preferences, similarly to the propositions by Martin & Huey (2008), but due to the different reason that the fitness benefits from adaptive enhancements on higher temperatures can overcompensate the lower losses of fitness in colder ones. The thermodynamic constraint, therefore, qualitatively changes the optimal preference strategy for facing variable environments. There is substantial amount of evidence suggesting the thermodynamic constraint is actually true, and one of the alternatives for it, the metabolic cold adaptation hypothesis (Wohlschlag 1964; Harper *et al.* 2000), which predicts that species from cold environments display higher metabolism as a compensation tool has failed to find empirical support (Clarke 1991; Harper *et al.* 2000; Brodeur *et al.* 2003; Peck 2016) although there are exceptions (Addo-Bediako *et al.* 2002; Brodeur *et al.* 2003).

The third alternative relative to the coadaptation hypothesis has been recently proposed by (Haupt *et al.* 2017). They are inspired by some empirical findings that the coadaptation of thermal optima and preferences can be modulated by other variables like for example resources availability (Halliday & Blouin-Demers 2017). If different life processes occur at different seasons or life periods, we expect them to have different optimum values, an idea that has been corroborated by empirical data (van der Have 2002; Bowler & Terblanche 2008; Dayananda *et al.* 2017), and therefore a single preference should not be universally optimal. They argue that the traits at which thermal preferences should more closely match the optima are those more impactful on the fitness of the species or organism, and there are much fewer tests of this hypothesis.

Huey & Slatkin (1976) developed theoretical models based to evaluate the thermoregulatory behavior from an individuals' perspective accounting for its' costs and benefits. They challenged some traditional views that thermoregulation was always benefic and that most organisms would always choose to thermoregulate "carefully". They assume that thermoregulating organisms opt for energetic costs (energy spent in moving among microclimates, risks in being more visible to predators and need to flee) in order to get some benefit (increase of performance). They predict that increased costs for thermoregulation, caused by local and species' conditions (e.g. forest areas with less available sun exposure, the organisms' body size), lead to optimal strategies in which species thermoregulate less frequently. The pattern is also dependent, however, on how much the environmental temperature regimes are close to the optimum value of the species, a feature that changes the possible benefits from thermoregulating. Therefore, organisms with low costs on thermoregulation, that are expect to thermoregulate more, may opt not to do it because the benefits would not be worthy if their environment is already very close to thermal optima. They also predict that thermal specialists should thermoregulate more carefully than generalists, because they obtain higher energetic benefits from this behavior. Those ideas have been further advanced by Vickers *et al.* (2011). They changed some assumptions of the model, using fitness gains instead of energy budgets and incorporating hot harsh temperatures to the framework (which previously only used cold ones). They predict that higher temperatures should lead to overall more careful thermoregulation, and that environments with temperature regimes more different to the species' optimum should also make them thermoregulate more.

Some other studies have performed modelling on thermoregulation by a biophysical approach (Connor 1999) to understand its' capabilities and the physical processes of energy fluxes through the body, especially for lizards. This type of models was also built for endotherms, to enhance understanding on how they can maintain high body temperatures even when facing high loss of heat to the environment (Rodríguez-Gironés 2002). Spatial-explicit models for understanding movement of individuals in thermally heterogeneous landscapes have also been developed (Fei *et al.* 2012), and they are useful for understanding the microhabitat usage of organisms (Walker *et al.* 2015).

THERMAL SENSITIVITY THEORY

When searching for generalities in thermal preferences across species, scientists developed the very important concept of Thermal Performance Curves (TPCs hereafter), that are special cases of reaction norms (Bullock 1955; Huey & Stevenson 1979; Reynolds & Casterlin 1979). There is a general pattern of a sigmoid or bell-shaped curve skewed to the right (or hotter temperatures) of the curve performance or process rate against temperature (Bullock 1955, Reynolds & Casterlin 1979, Huey & Stevenson 1979). This curve (figure 1) aggregates the most important and general variables describing a species' thermal sensitivity: temperature optima, tolerance and performance breadths and critical minimum and maximum temperatures (Huey & Stevenson 1979). The steep decrease in performance associated to hot temperatures is viewed as worst effect on performance for overheating, probably because of protein denaturation.

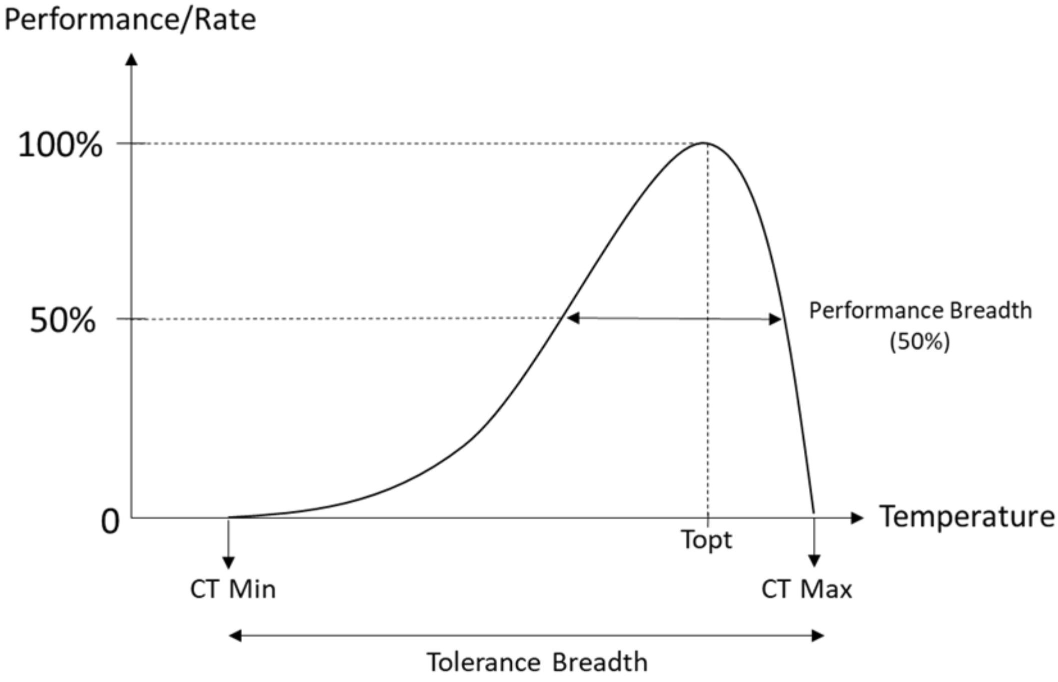

Figure 1: The representation of a Thermal Performance Curve. CT Min and CT Max are, respectively, the critical thermal minimum and maximum (Also called Lower and Upper Thermal Limits), and they delimitate the range at which performance is positive. Tolerance breadth is defined by the difference between the critical maxima and minimum. Performance breadth is the difference between critical limits for a determined threshold of performance (the performance breadth for 50% of performance is exemplified in the figure). Temperature Optimum (Topt) is the Temperature at which the performance is maximal.

The development of the TPC concept granted theorists a useful framework for building models and propositions. Most of the questions regarding TPCs were related to either its' evolution, biological constraints or to what extent can they be applied to real systems. For example, Huey & Stevenson (1979) proposed that some aspects of the TPCs are more interesting from an ecological point of view, as others were interesting from a physiological point of view. They stated that temperature optima and performance breadths seem to be more related to organisms' day-to-day challenges, because they usually thermoregulate and are not present in places which pose relatively extreme temperatures, and therefore these parameters should be more critical when limiting life processes and organisms' fitness. It was argued that, as organisms should avoid temperature extremes, tolerance is less impactful on their finesses, but more important from a physiological and cytological point of view, as it is more related to the tissues and fluids capabilities and to the biophysical and chemical limits of performance.

Questions regarding TPCs variability were also developed. Huey & Stevenson 1979 asked if TPCs are variable depending on the life process involved, in other words, if there are different parameter values for different processes in the same species or individuals. This reasoning led to question if the parameters may be also affected by seasonality and change through an organisms' life history. Two general hypothesis that arise on how TPCs are constrained biologically were proposed: the "Hotter is Better", and the "Jack-of-All Temperatures is a master of none" hypotheses (Huey & Kingsolver 1993). If higher temperatures allow higher energy usage and metabolism, as poses the thermodynamic constraint, species or individuals on higher temperatures should present overall higher fitness than their counterparts from colder places, and therefore, "hotter is better". Besides, if there are allocation tradeoffs in the strategy adopted by an organism or species, adapting for a higher performance in some temperature should lead to lower performance in other temperatures, therefore, there should not be a "Jack of all temperatures", or in other words a "Jack of all temperatures is a master of none".

Huey & Kingsolver (1993) advanced on TPCs possible variability, and proposed some patterns by which TPCs may evolve, based on which mechanisms may constrain the curves. The jack-of-all temperatures hypothesis leads to a scenario in which species must decrease performance in some temperatures so they can specialize in other ones, what leads to changes in optimum values or in the curves getting "thinner", the latter outcome representing a specialist-generalist tradeoff. Otherwise, if species can enhance performance in some temperatures without trade-offs, probably due to new mutations and conformations of proteins, that would lead to broader curves with larger performance breadths, and curves would increase in volume (figure 2).

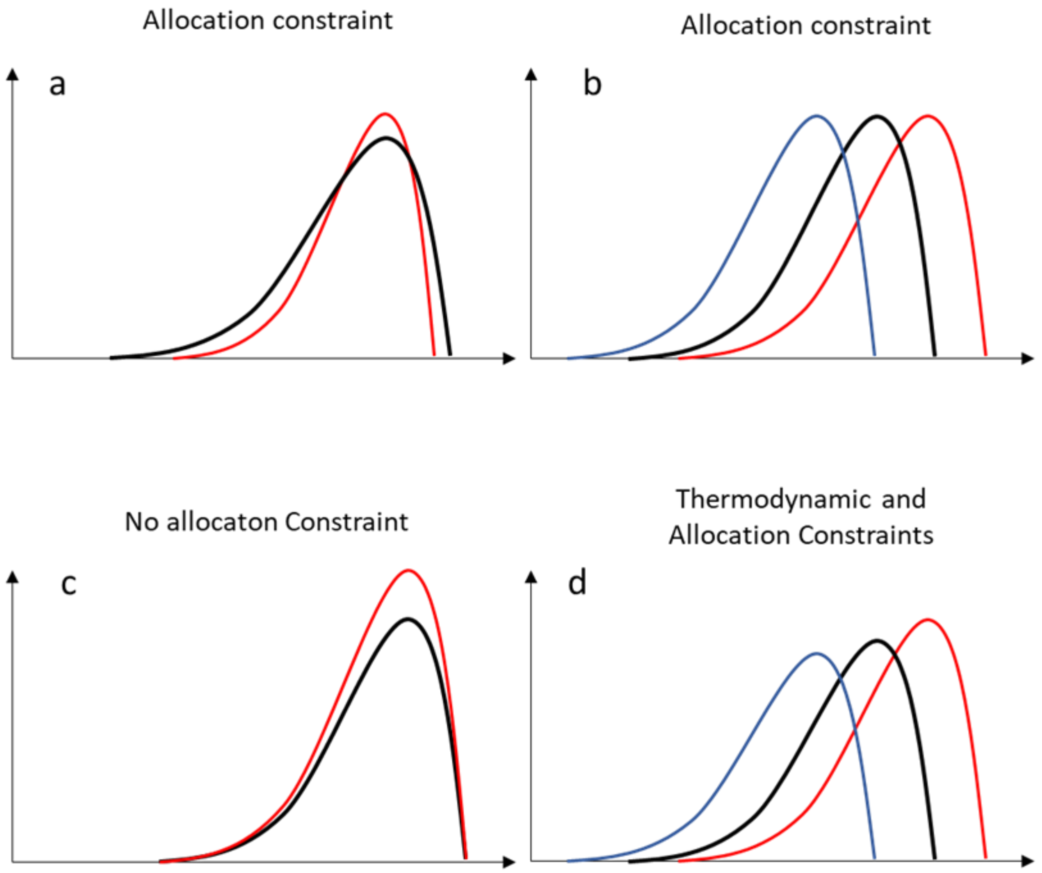

Figure 2: Variation patterns in TPCs expected by different constraints. a) Constrained by allocation trade-offs, species in red is a thermal specialist, it evolved a higher performance in optimum temperature at the cost of decreased performance and tolerance breadths. b) Also constrained by allocation trade-offs, species are adapted to different thermal regimes. Red species is adapted to a hotter environment, and blue species adapted to a cold environment. c) If there is no allocation constraint in thermal adaptation, species should be able to increase performance without losses, and the area under the curve would increase. d) Species are constrained by allocation trade-offs but also by thermodynamics. They are specialized to different thermal regimes, but species adapted to warmer regimes display higher possible performance.

TPCs were also explored through the use mathematical models of tolerance theory. The classic frameworks for modelling reaction norms were called optimality models, with some works especially important for Thermal Ecology (Lynch & Gabriel 1987; Gavrilets & Scheiner 1993). These models had the similar objective of understanding how the shape of tolerance curves (for various factors, not only temperature) and its' relationship to environmental variability should impact fitness and the evolution of organisms. Lynch & Gabriel (1987) assumed an asexual population exposed to a gradient with temperature variability in space and time, and they differentiate from contemporaneous niche width models by assuming the possibility of within-species variation in tolerance parameters. Their objective was to find the optimal strategies that species should adopt on their tolerance ranges to be more resistant to variable environmental stress. They concluded that environmental variation within generations is more important than variation among generations, selecting for more broadly tolerant curves. Spatial variation is also important, selecting for broader tolerances but only when temporal variation occurs within generations. Their work suggests that species must be tolerant to the range of temperatures that they experience in their life history as a whole.

The framework of tolerance theory was later applied specifically to thermal tolerance (Gilchrist 1995). He developed from the more advanced frameworks of thermal ecology, and incorporated different functions for tolerance and for performance processes. He assumed that tolerance is related to an organism’s survival in a given temperature, and performance is given by the result of other life processes such as growth and reproduction following the already known framework of TPCs. This change led to a pronounced outcome of thermal specialization, and the models favored specialist genotypes even when temporal variability in temperature was high. Briefly, they show how specialists can show overall higher fitness than generalists by benefiting from large fitness enhances during small time periods. This result is in discordance with that from Lynch & Gabriel 1987, which show preference for broader performances in the face of variation. Also, Gilchrist (1995) predicted selection for broader curves only when temporal variation in temperature was strong among the generations.

An interesting development from optimality models was performed regarding the capabilities of species for tracking climate change (Huey & Kingsolver 1993). When faced by climate change, species can adapt to new environments or track that change through changes in their ranges (Leroux *et al.* 2013). The question on how much those responses is possible is totally dependent on the genetic basis of TE and the heritability of TE traits. Huey & Kingsolver (1993) developed a genetic model specifically for TE, assuming thermal optima and performance breadths in a population experiencing a gradually changing environment. They analyzed if thermal breadth and its’ underlying genetic variation had some influence in the capacity of species to adapt to climate change. Due to a specialist-generalist constraint in their TPCs, large thermal performance breadths also display lower maximum performance, and this causes the tracking of climate change to be slower, as more accurately adapted population would display less fitness benefit from being so. This suggests that generalist species should be less able to change their ranges. Species that are highly specialized, however, would not be able to track fast changing climates due to elevated impacts caused by smaller magnitudes of changes. Under the absence of any relationship between thermal breadth and genetic variability, species more able to track climatic changes are the ones with intermediate thermal breadths. When they assume that larger breadths might display larger genetic variation, this result is qualitatively different, as genetic variation facilitates the capacity for environmental tracking, and larger performance breadths were able to track faster environmental changes. Those results are very important from a conservation and management point of view, although due to their nature they are very difficult to validate.

SCALING UP IN ECOLOGICAL ORGANIZATION

Theoretical arguments have been developed regarding the effect of temperature from community and macroecological perspectives. The effect of temperature on species interactions has been studied both theoretically and empirically, and theoretical advances have been obtained. Some advances were reached by studying predator-prey dynamics. Models were used for predator-prey systems explicitly considering their TPCs (Mitchell & Angilletta 2009; O'Connor *et al.* 2011; Dell *et al.* 2014). Those models were able to offer important predictions, like that changes on temperature regimes might cause extinctions on prey due to overexploitation (Dell *et al.* 2014) and changes of equilibrium in the resulting population dynamics of the systems (O'Connor *et al.* 2011). Mitchel & Angilletta 2009 incorporated game theory in spatially explicit models, and predicted that habitat choice of prey must be associated to predator lethality. More efficient predators should influence prey to be thermal generalists, and less effective predators should influence prey to be thermal specialists. This should happen because specialists would tend to occur in places with similar environmental characteristics, and therefore their occurrence should be more predictable for predators. Other than for predation interactions, important propositions have been elaborated, as for example how temperature might affect invasion processes through priority effect. If "Hotter is Better", higher temperatures cause higher metabolism and overall performance, and therefore species which invade environments first should alter the invaded environment at faster rates in warmer regions (Rudolf & Singh 2013; Grainger *et al.* 2018). This priority effect is important for invasion processes, but it is also impactful for understanding the strategies on species' phenology. The interest of understanding how temperature might directly or indirectly affect general interaction outcomes has led to important frameworks and systematizations of the possible results (Gilman *et al.* 2010; Kordas *et al.* 2011).

There has also been effort on understanding the effect of temperature on food-webs. Higher basal metabolism, caused by temperature, increases the energetic needs of organisms, and therefore a lesser amount of energy is expected to flow through trophic levels in food webs of hotter environments (Clarke 2003). There has been some experimental evidence for this effect (Petchey *et al.* 1999; Kordas *et al.* 2011). This leads to the hypothesis that upper trophic levels are expected to be especially impacted by climate change due to decreases in energy availability.

MACROECOLOGICAL CONSEQUENCES

Some hypothesis on TE were made after observations of experimental results or patterns. One of the most prominent patterns of this case is the temperature-size rule (TSR). It is widely known that the majority of ectotherms, unicellular or multicellular, display larger body sizes when reared in cold environments or experimental treatments (Atkinson 1994; Gilbert & Raworth 1996). This pattern at first seems counter-intuitive, because hot environments increase organismal metabolism and should facilitate growth and larger sizes. Differently from other investigations in TE, from which scientists needed to test the patterns predicted by theory, in this case they needed to propose possible explanations for this already perceived pattern, similarly to the Latitudinal diversity gradient discussed below. This pattern has been discussed as either the effect of biological constraints (Berrigan & Charnov 1994; Angilletta *et al.* 2003; Walters & Hassall 2006) natural selection (Kozłowski *et al.* 2004; Arendt 2011, 2015; Edeline *et al.* 2013; Vangansbeke *et al.* 2020). Modelling studies have shown that discrepancies between enthalpies and thermal sensitivities for growth and developmental processes can lead to the TSR (Berrigan & Charnov 1994; Walters & Hassall 2006). There is, however, lack of evidence for those suggestions (Angilletta & Dunham 2003). Empirical studies have shown, in the other hand, evidence that larger bodies confer important fitness advantages in cold environments. Those advantages happen due to higher fecundity (Arendt 2011, 2015), lower predation probability and mortality (Kozłowski *et al.* 2004; Edeline *et al.* 2013) and higher predatory potential (Vangansbeke *et al.* 2020). This evidence, however, still cannot be directly linked as a mechanism for the TSR, and the puzzle is still unsolved. There has been discussion about whether the TSR is the result of a single, general mechanism or if it can have multiple explanations for different groups of organisms (Angilletta & Dunham 2003). There has been some effort in finding other factors influencing the TSR, as it is for example mediated by oxygen availability in aquatic ectotherms (Hoefnagel & Verberk 2015), diet limitations in caterpillars (Lee *et al.* 2015) and can be related to age in Artemia (Forster & Hirst 2012).

Beyond that, the search for explanations on the latitudinal diversity gradient (LDG) also relate to thermal ecology. One of the main hypotheses for the LDG accounts for evolutionary speed (Mittelbach *et al.* 2007). It was formulated that lineages occurring in lower latitudes present higher rates of diversification, and this could explain the higher diversity in those latitudes. There has been effort to find what mechanisms could lead to that pattern, and temperature has been proposed as a possible cause for it. One of the most prominent propositions of a mechanism is related to the Metabolic Theory of Ecology (Brown *et al.* 2004), states that temperature might affect speciation rates through collateral effects of metabolism. Higher metabolism results in higher production of chemical by-products that could be harmful to the DNA structure and therefore increase the frequency of mutation (CITE). Another hypothesis stands that the mechanism might be the effect of cold temperatures on proteins stability (Puurtinen *et al.* 2016). They argue that, as cold adapted proteins have lower physical stability, they also display a lower chance that the effect of a possible mutation will be benefic. This is because mutations are random, and cold-adapted proteins would more frequently result in more unstable and even deleterious proteins. Clarke & Gaston (2006) discussed the effects of energy and temperature on diversity, and the hypothesis that warm environments are more amenable and therefore more diverse. They counter-argument, based on earlier ideas (Hutchinson 1959), that being more amenable or tough is relative to each species historical adaptations, and therefore this hypothesis is not exactly objective and difficult to validate. Stevens (1989) proposed that the seasonality of temperature might actually be the mechanism for the gradient, a process reviewed by Clarke & Gaston (2006). If low latitude species experience lower environmental variability, they would be highly specialized, with smaller ranges and therefore more species would be able to fit the environment. His hypothesis has been dismissed due to evidence from comparisons of terrestrial and marine gradients, as they show different patterns of variability (Clarke & Crame 2010), although possibilities are still open (Clarke & Gaston 2006).

Although those ideas for explaining the LDG are not originally related to the paradigms of TE, I find it possible that they could have impacts and relate to other questions in the field. As I will discuss later, there has been effort in understanding the velocity of the evolution of thermal traits, and this problem is directly linked to the proposed mechanisms for the LDG. It is also possible that the experimental and empirical frameworks already designed for thermal ecology might be useful for testing and exploring those hypotheses, especially the rearing and selection experiments.

All the theoretical propositions ensured he field of thermal ecology to be very throughout the years. Some of those questions led to enhancements and developments of new experimental approaches, and as knowledge accumulated some other interesting phenomena appeared to need explanations. In the following section I will discuss how experiments were designed and enhanced, the new questions they posed and some of the empirical synthesis achieved.

Experimental and Empirical Approach

Thermal ecology (or thermal biology) began to develop itself based on experiments. Early studies on thermal ecology focused on experiments for understanding species thermoregulation, acclimation capacities, preferred temperatures and critical thermal maximum and minimum (Bogert 1949; Bullock 1955; Brett 1971; Huey & Stevenson 1979). This curiosity was probably inspired by observations of the behavior of organisms, as for example lizards basking in the sun for heating and snakes becoming lethargic in cold temperatures. Because the effects of environmental temperature are more conspicuous in ectotherms, insects, lizards and amphibia are groups highly studied in the area, with various model species for the field, as for example lizards and *Drosophila* (Brattstrom 1963; Hoffmann *et al.* 2003). At that time, thermal ecology was approached from both a physiological and ecological point of view. The physiological approach was more centered to the functioning and causes of thermal sensitivity and tolerance. Experiments with this approach were usually performed directly on cells and tissues, isolated from the organisms (Huey & Stevenson 1979). Those experiments usually exposed muscle tissue to different temperatures, and analyzed how temperature impacted muscle spasms (standardized by SO, spasm onset) or changes in activity (Lutterschmidt & Hutchison 1997). Experiments centered to an ecological approach were focused on how temperature affected whole organism functions (Beitinger & Fitzpatrick 1979; Huey & Stevenson 1979). There were two dominant approaches for these studies: either exposing organisms to a wide array of environmental temperatures and letting them choose which one they would prefer (finding the organisms' preferred temperature), or manipulating environmental temperature and analyzing impacts on performance of locomotion and sensing abilities (LRR, loss of righting response) (Lutterschmidt & Hutchison 1997). In order to study more complex and broad organismal functions such as growth rates and reproduction, rearing experiments were performed in larger temporal scales, and the need to understand the evolution of traits caused breeding and selection experiments to also take place in TE.

As thermal ecology developed, questions started to delve on biological mechanisms and hypotheses, going beyond the descriptions of species' preferences. It was recognized that thermal preferences were species-specific (Bayard H. Brattstrom 1963; Beitinger & Fitzpatrick 1979), and this led to questions about how they can evolve (Bogert 1949) and their relationships with the biogeography of the species (Bullock 1955; Beitinger & Fitzpatrick 1979). Brattstrom 1963, for example, concluded that thermal characteristics are not only species-specific but restricted to phylogeny in other levels (the majority of amphibians thermoregulated when exposed to harsh temperatures, but salamanders did not). He also concluded that frogs do not present an optimum value for temperature, but rather an interval of optimum temperatures, and discussed how thermal ecology may affect other levels or ecological organization, hypothesizing that it is because of thermal preferences that there are no frogs living on areas with mean temperatures below 15oC. Beitinger & Fitzpatrick (1979) also questioned if thermal preference has implications in life history and species occurrences. Beck 1977 began investigating how thermal preferences interact with photoperiod to explain species behavior, and found that thermal regimes and photoperiod are, a better predictor of diapause occurrence in flies. Dawson 1975 contributed to the field discussing the importance of understating intraspecific variance in thermal sensitivity of organisms, and joined evidence to corroborate that species' preferred temperatures is also the temperature in which the performance of various processes is highest, proving that life history and thermal responses evolve together, adding evidence to some of the important theoretical questions initially posed.

As time passed, ideas became more complex, older experimental designs were criticized and enhanced and novel questions appeared. It became acknowledged that photoperiod, for example, is an important factor influencing thermal ecology (Beck 1977). Species use photoperiod as cues for the conduction of some life processes and daily activities, and experiments thus should include its effects on their designs (Lutterschmidt & Hutchinson 1997). Another fact which was neglected on older studies is acclimation (Lutterschmidt & Hutchison 1997; Rezende *et al.* 2011) for discussion). When experimenting on individuals, the temperatures to which the individuals were exposed prior to capture or the experiment processes have important impacts on their performance and even in their temperature optimum (Seebacher & Grigaltchik 2015). Acclimation itself is also not simple: the alterations caused by acclimation on physiology may be dependent on duration (for how much time was the individual exposed to a harsh temperature) and intensity (how harsh is the temperature) of exposure (rezende *et al.* 2011). All those intricacies became explicit on experimental designs (Lutterschmidt & Hutchison 1997; Chown *et al.* 2009).

An important framework developed for understanding acclimation is the thermal tolerance polygons (figure 3). They are a direct consequence of the fact that acclimation affects experiments' results. To my knowledge, the first description of this approach was produced by Fry (1971), and it has been applied especially to fish (Bennett & Beitinger 1997; Hernández & Bückle 2002; Eme & Bennett 2009; Kır *et al.* 2017). The polygons are a description of how tolerance values (CTmin and CTmax) change related to different acclimation temperatures, so that "a trapezoidal figure bounds the zone of thermal tolerance" (Fry 1971). Inside this polygon of survival tolerance, it is also possible to draw other polygons limiting other life processes such as reproduction and growth. It is also possible to differentiate between tolerance (zones of temperature in which individuals can survive in long-term) and resistance zones (zones which affect long-term longevity, but do not cause short term death). A conceptually similar idea, is that of thermal performance landscapes (figure 3). They are an expansion of standard thermal performance curves to incorporate intensity of thermal stress in a three-dimensional model (Rezende *et al.* 2014).

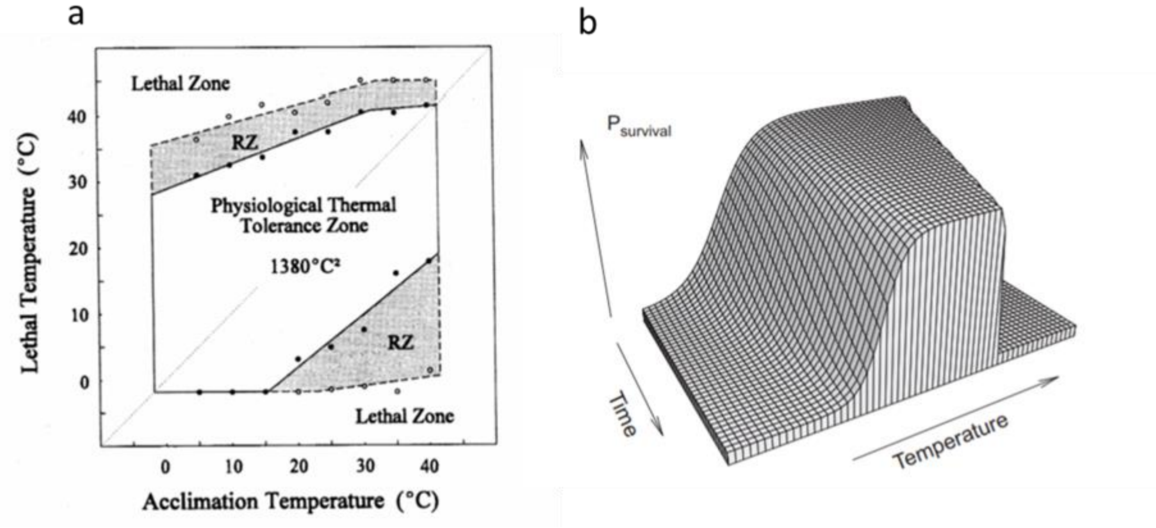

Figure 3: Examples of thermal tolerance polygons (a) and thermal performance landscapes (b). a) The thermal tolerance polygon extracted from for a fish (Bennet and Beitinger 1997). Lethal temperatures are assessed under different acclimation temperatures. With this framework it is possible to differentiate between tolerance zones (white central area, in which species can survive at long term), resistance zones (grey areas, under which species can survive at short term but have their longevity altered) and lethal zones (in which species cannot survive at short term). b) Thermal performance landscape conceptual graph extracted from Rezende *et al.* 2014. Exposure time to thermal stress interact with the magnitude of temperature to predict the final probability of survival.

The complications go further, as for example Rezende et al 2011 discussed that the health conditions of organisms can bias studies' results, as individuals from certain temperature treatments may get dry in the heating process. Individuals with access to high quality food or that are more well fed may also have different thermal responses to thermal stress (Sinclair 2015; Hu *et al.* 2019). Van der Have 2002 experimented on organisms of different age classes, and showed that controlling organisms ages is also important for unbiased experiments, an issue also discussed by Bowler & Terblanche 2008. Sharpe & De Michelle 1977 discussed, based on modeling the day-degrees concept, that experimenting on a wide range of various temperatures is more adequate to "realize the full potential of the thermodynamic approach to development" (Sharpe & DeMichele 1977). There are experiments showing that intensification of metabolism, which may be caused by elevation of temperature, causes more need of oxygen (Hoefnagel & Verberk 2015; Walczyńska *et al.* 2015). Therefore, when assessing marine/aquatic species or the effects of altitude, oxygen dissolved in water or thinner air may impact performance on high temperature treatments, which may lead to interpreting what is actually stress by lack of oxygen as thermal stress. Some studies found that organisms respond differently to constant and variable thermal regimes, on both daily and broader scales, and they bring the question if experiments on constant temperatures, which are rarely found in nature, can be trusted and applied (Bartheld *et al.* 2017).

The statistic tools used for assessing thermal ecology also changed through time. At first, there has been some trials in order to find what would be the best equations to model the classical framework of TPCs. Some studies dealt with this directly by addressing what equations best fit performance data (Shi & Ge 2010; Tomlinson 2019), also considering the possibilities of overfitting the data (Angilletta 2006), and there has been systematic reanalysis of older experiments showing that scientists not always use the models which best depict the data (Quinn 2017). Appropriate statistical tests for this approach has also been discussed, and in this case the use of linear regressions, ANOVA and high complexity overfitting models have been criticized (Angilletta 2006; Bulté & Blouin-Demers 2006; Shi & Ge 2010). Studies addressing thermoregulation had an important enhancement in their statistical designs through the usage of physical copper models as null models or comparison of thermoregulation capacities (Hertz *et al.* 1993; Seebacher & Shine 2004; Christian *et al.* 2006; Ortega *et al.* 2016). Beyond that, interesting propositions have been done on how to use data to find intra-specific variation in TPCs (Izem & Kingsolver 2005; Seebacher *et al.* 2015a; Ramakers *et al.* 2019). There has also been effort on unifying different mathematical measurements of tolerance and performance, in order to help and enhance the possibilities of synthetical studies comparing different experiments and species (Cooper *et al.* 2008; Camacho et al. 2018).

In TE, as knowledge advanced, so did the need to bring together biogeography, genetics, phylogenetics and more diverse types of experimentations. The acknowledgement that there is local adaptation for thermal preferences, for example, is very old (Bullock 1955, Dawson 1975) and links thermal ecology to biogeography. One method to asses this pattern is through comparing experimental results from individuals of populations from different locations, altitudes or biomes (Oyen *et al.* 2016; Terra *et al.* 2018; Trochet *et al.* 2018; Hodgson & Schwanz 2019; Hu *et al.* 2019; Litmer & Murray 2019; Algiriyage *et al.* 2020). This biogeographical approach to thermal ecology makes the variance in the results of experiments interesting and useful. In order to understand how thermal ecology of individuals scales to population and geographical levels it is important to understand local adaptation inside the species' ranges and the intra-individual variance in the populations. Local adaptation has been empirically assessed both by rearing experiments but also by morphological and physiological assessments (Litmer & Murray 2019 for lizards in invasion sites, Oyen *et al.* 2016 for thermal limits of bumblebees adapted to altitude, Rochet *et al.* 2018 for thermal preference and altitude in reptiles, Hu *et al.* 2019 for feeding and metabolic rates in altitudes, Algyriyagi *et al.* 2020 for traits of anurans, Clarke 1991 for morphology and cytology of fish).

In order to understand how thermal ecology evolves, studies also incorporated genetics/selection and phylogenetics approaches (Huey & Kingsolver 1989; Angilletta *et al.* 2002). Understanding the genetic basis and heritability of thermal preference and sensitivity is important to understand their evolution, their constrains and intra-specific variation. The genetic basis of thermal ecology has been assessed directly through identification of genes/genotypes and proteins expression, (e.g. Meffe *et al.* 1995; Sørensen *et al.* 2001; Dolgova *et al.* 2010), but also indirectly by measuring variance among different populations, lineages and siblings of organisms (Sinervo & Adolph 1989; Kingsolver *et al.* 2004; Latimer *et al.* 2011). Breeding and selection experiments were developed for assessing the genetic basis and heritability of TE. Breeding experiments consist on measuring the heritability of TE traits through control of breeding of organisms from different locations, altitudes or families (Ibrahim & Quick 1994; Perry *et al.* 2005). Selection experiments expose a family or population of organisms to a gradual change in temperature for several generations as the change ins organisms' phenotype is tracked (Ibrahim & Quick 2001; Morley *et al.* 2017). Overall, there has been some success in identification of relevant parts of the intra-population/familiar variation as result of genetics (Sinervo & Adolph 1989; Kingsolver *et al.* 2004). Beyond that, studies also found evidence for genetic independence of some traits (Sørensen *et al.* 2001; Hoffmann *et al.* 2003) and for benefits from heterozigozity for thermal tolerance (Meffe *et al.* 1995). Breeding and selection experiments have an overall conclusion of genetic additive effects on traits (Perry *et al.* 2005 for upper thermal tolerance in trouts, Ibrahim & Quick 2001 for membrane thermal stability of wheat). Due to the fact that variation in thermal ecology traits and that they are possibly expressed by multiple genotypes, identification of genes responsible for them has been difficult, but has been performed in some cases (Dolgova *et al.* 2010). There are new methodologies for analyzing genotypes being developed to deal with this issue in particular (Yap *et al.* 2007).

Although early studies showed phylogenetic constraints on phenotypes, studies still needed to answer the velocity by which those changes evolved, the genetic basis of this evolution, the coadaptation in these processes and relate thermal ecology to the evolutionary history of organisms. Beyond finding the patterns and co-adaptations in thermal ecology, we also need to address if those patterns are results of physical constraints or are adaptive. If thermal preferences of species are highly adaptive or labile, we expect species to have their preferences highly correlated to the environment in which they live, because they had enough generations and time to adapt to that environment. If the preferences are not adaptive or thermal niche is highly conserved, phylogenetic signal on these traits should be high. The use of detailed phylogenetic information can help understanding the evolution of species' traits (Berkum 1986; Nespolo *et al.* 2017), and this has been performed both for experiments and meta-analysis. Those studies were able to prove some species present some highly labile thermal traits, for example metabolic rates of amphibians that evolve faster than Brownian motion null models (Nespolo *et al.* 2016), thermal maxima in intertidal crabs (Stillman & Somero 2000), the thermal preference and thermal optima in skinks (Huey & Bennett 1987) and the low lethal temperatures for crabs and lizards (Grigg & Buckley 2013; Faria *et al.* 2017). Other traits, however, displayed high phylogenetic signal and low adaptability, as for example thermal maxima for drosophila, crabs and terrestrial ectotherms (Sunday *et al.* 2011; Kellermann *et al.* 2012; Faria *et al.* 2017) and the development of Odonata eggs (Pritchard *et al.* 1996). Interesting co-adaptation patterns between thermal characteristics have been found, for example preferred and optimum temperatures are positively correlated on skinks (Huey & Bennet 1987), and thermal minimum and maxima are not coadapted in crabs and lizards (Grigg & Buckley 2013; Faria *et al.* 2017). Phylogenetic information associated to thermal ecology has also been used to discuss ancestralism of traits and possibilities of geographic origins for different taxa (Huey & Bennett 1987; Pritchard *et al.* 1996).

Experiments also developed to incorporate other questions like the interplay of TE and ecological interactions. Microcosm experiments, which simulate meta-populations in temperature gradients, have successfully demonstrated that environmental temperature changes the outcome of competition and the dominance of communities of ants, microalgae and Drosophila (Davis *et al.* 1998; Wittman *et al.* 2010; Hillebrand 2011). The interaction of TE with competitive process has been evaluated in field studies. For example, TPCs have been shown to be relevant in the dominance outcome after fish introduction in lakes (Hein *et al.* 2013), and the thermoregulation of lizards through selection of hot spots on rocks is performed in a pattern in which they avoid competition (Pafilis *et al.* 2017). Parasitism also have been proved to influence thermal preference, though a process sometimes referred to as "behavioral fever". As an example, newts select warmer body temperatures when are parasitized (Sherman 2008). Experiments also developed for finding other relevant factors that interact or modulate thermal responses of species. Other abiotic factors like oxygen availability (Hoefnagel & Verberk 2015; Walczyńska *et al.* 2016) and toxic substances (Hallare *et al.* 2005) has been found to influence TE responses, and it was shown that TE is correlated to other behavioral and morphological characteristics of the organisms, like melanism and aggressiveness (Stapley 2006; Clusella Trullas *et al.* 2007; Hassanalian *et al.* 2017).

Synthetical Studies

Due to tremendous efforts in experiments and species comparisons in TE, we are able to draw important synthetical conclusions from it. At first, there has been mixed support for the coadaptation hypothesis, both optimally and sub-optimally (Dawson 1975; Huey & Bennett 1987; Huey & Kingsolver 1993; Halliday & Blouin-Demers 2017; Patterson *et al.* 2017; Crickenberger *et al.* 2020). It is clear that preference and sensitivity are coadapted in various taxa, sometimes optimally and sometimes sub-optimally, but we cannot conclude that it is an overall general pattern. This suggests that for some species temperature might be a critical factor for final fitness, but also suggests that some species, which do not present the coadaptation hypothesis in any of its' variations, might face other more important factors constraining fitness.

Conclusions about the evolution of thermal ecology are also possible. Overall, thermal sensitivity and preference are adaptive and often highly labile (Berkum 1986; Stillman & Somero 2000; Araújo *et al.* 2013b; Nespolo *et al.* 2017; Terra *et al.* 2018), and some studies suggest thermal preference evolves faster than sensitivity (Huey & Bennet 1987), implicating a higher lability of behavior over physiology. Also, there is a clear pattern for a higher lability and variation in lower thermal limits (CTmin, cold tolerance) than for upper thermal limits (CTmax, heat tolerance) (Sunday *et al.* 2011; Kellermann *et al.* 2012; Araújo *et al.* 2013a; Grigg & Buckley 2013; Faria *et al.* 2017; MacLean *et al.* 2019). There is no trend about the correlation between Upper and Lower Thermal tolerances, as some studies confirm correlations (Clarke 1991; Kellermann *et al.* 2012) and others find independence (Sørensen *et al.* 2001; Grigg & Buckley 2013).

Relationships between thermal breadth and environmental variation have also been successfully elucidated, as generally thermal tolerance increases with latitude, and this relationship is different for terrestrial and marine organisms (Sunday *et al.* 2011; Sheldon & Tewksbury 2014; Bartheld *et al.* 2017; Rohr *et al.* 2018; MacLean *et al.* 2019). Thermal tolerance is also negatively correlated to organismal complexity, as was elegantly showed in a meta-analysis with a comparison ranging from bacteria and protozoa to reptiles (Storch *et al.* 2014). There is accumulated evidence suggesting that evolutionary variation is dependent on phylogenetic scale (Yamahira & Conover 2002; Clarke & Fraser 2004; Gvoždík & Van Damme 2008; Phillips *et al.* 2014). Variation tends to occur on optimum and following the "jack of all temperatures is a master of none" trade-off within the species, while among the species variation usually changes overall performance of organisms, following the "Hotter is better prediction" and the thermodynamic constraint. This probably happens because, given enough evolutionary time for speciation, species are able to develop benefic mutations which do not follow the allocation trade-off. Given little evolutionary time, genetic variation is probably not big enough to cause this type of variation, and an allocation trade-off is present.

Conclusions

In this work, I discussed the theoretical basis of Thermal Ecology and how scientists studied the field empirically. The theoretical foundations are strongly based on optimality and thermoregulation models built from state-variable models. More recently, theoretical grounds have escalated to community and macroecological scales. There is a lot of empirical information in the field, accumulated by decades of experimentation and developments of new empirical and analytical approaches.

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CHAPTER 2 – POPULATION ECOLOGY EMERGENT FROM ENERGY BUDGETS AND THERMAL ECOLOGY THROUGH AN IBM

Abstract

Mathematical models have always played an important role for theoretical development in ecology. As computational power advanced, so did our opportunities for simulating and evaluating more complex and detailed systems. It is often pointed that more complex and realistic models might not be adequate for theoretical explorations because they allegedly lack generality. Our objective here was to develop an individual-based model for population dynamics, able to generate general predictions, which incorporates detailed processes of self-regulation and relationships with the environment. For that, we used concepts from thermal ecology and DEB theory to explore macroecological patterns from randomly generated species. In this model, population abundance patterns emerged from how individuals of different species (of different DEB parameters and body sizes) interacted with the environment (different temperature regimes and resources availability). Our results reinforce the idea that we should be cautious when escalating individual-level information to higher levels of biological organization, as patterns on this scaling might be very complex. Our model generated a realistic system, that could be able to advance knowledge about other more specific ecological questions.

Keywords: individual-based model, temperature, population dynamics, energy budgets, mechanistic models.

Introduction

Various types of human impacts on nature are pressing our needs to develop prediction and theoretical understanding of systems in ecology. Mathematical models or simulations play a very important role for achieving those goals. In the last decades, the developments of technology and computational power allowed us to explore models that are much more complex, and debate has heated on the capabilities of this type of approach. There has been a rise in usage of the individual-based approach (IBMs) (Judson 1994; Grimm *et al.* 1996; Grimm 1999), both for theoretical and practical questions (Deangelis & Grimm 2014), and discussion on comparing them to classical differential-equation or state-variable models has taken place. Usually, modelling approaches are discussed by their capabilities within the spectrum of generality and realism (Judson 1994; Grimm *et al.* 1996). Those two attributes were usually seen as total opposites, although this has been discussed and criticized (Zeide 1991; Grimm *et al.* 1996; Deangelis & Grimm 2014; Johnston *et al.* 2019). Biological systems are highly complex, and if we implement models with the detail needed for accurate predictions, they might lose the ability to address several circumstances or be useful for a variety of species. The debate around the realism-generality spectrum seems to have created a dichotomy in models' objectives, in which some should be built around "predictions" while some should be built for "understanding" and theory. Deangelis & Grimm (2014) discussed the differences between those two usages of IBMs, defining them as pragmatic (when very complex/detailed oriented to practical questions and prediction) or paradigmatic (when more general and oriented to theory and generalization). IBMs have been applied to a variety of practical questions, e.g. (Mazaris & Fiksen 2005) for conservation of turtles, (Choi *et al.* 2006) for agricultural impacts of slugs' populations, (David *et al.* 2019) and (Beaudouin *et al.* 2015) for ecotoxicology, (Arnould-Pétré *et al.* 2021) for climate change impacts on sea urchins, and, to a lesser extent, to paradigmatic questions like advances on community ecology (Giacomini *et al.* 2009, 2013), food webs and epidemiology (Deangelis & Grimm 2014), predator prey systems (Thierry *et al.* 2014), movement ecology (Travis *et al.* 1998; Malishev & Kearney 2017) and population dynamics (Uchmánski 1999, 2000). However, the opinion that we should insist on trying to build models that are both more general and realistic seems to have been, overall, strengthened.

Much has been elaborated on what are the limitations and advantages of IBMs for theoretical questions and generality (Judson 1994; Grimm *et al.* 1996; Deangelis & Grimm 2014), and also much has been proposed to deal with those limitations (Grimm *et al.* 1996, 2010; Deangelis & Grimm 2014) and to fully explore their advantages (Uchmánski & Grimm 1996). Some features of IBMs help at building more realistic ecological predictions. The most noticeable one is probably the capacity to capture important details of life history in an adequate time scale (Grimm 1999). This is very important for the study of population dynamics. The way they deal with individual variability is crucial (Grimm 1999). For example, Uchmanski (1999) and (2000) uses IBMs in a paradigmatic approach, to understand how variability affects stability, and important results were generated, which probably could not have been achieved through classical models. IBMs also allow to explicitly model organisms' interactions, which can be important when asking questions about competition or adaptation. Incorporation of adequate temporal and spatial scales in IBMs is also advantageous, as some works have shown (Letcher *et al.* 1998; Wang & Grimm 2007), and this is of utmost importance for adequate validation and testing of generated hypotheses. IBMs also display Improvements when modeling low population numbers in which populational means or statistical distributions may be misleading (Judson 1994). When talking about IBMs limitations, some very conspicuous ones also arise. IBMs may require a lot of data for parameterization and parameters, which may be bad for theoretical purposes (Judson 1994). Also, the lack of a common framework (mathematical equations, in the case of classical models) and insufficient communication and clarity on descriptions may hamper how we compare models to each other, and this way models become disconnected and less general. As they can be models with a high level of complexity and detail, their results will often display those same characteristics, and often will be hard to evaluate.

In order to really utilize the benefits of IBMs and not get lost in complexity, some cautions should be taken into account. At first, we must choose wisely which aspects of reality should be modeled. Pattern-oriented modelling is a nice approach to that (Grimm *et al.* 1996), which means developing models with the goal of reproducing patterns observed in nature, and therefore exploring and incorporating the mechanisms that more clearly generate those patterns. We should focus on a mechanistic approach to the sub-models and models' concepts, so that a better capacity for prediction doesn't contrast to understanding (Grimm *et al.* 1996). It is also important to maintain track of spatial and temporal realistic scales, so accurate testable and understandable predictions can be generated (Judson 1994; Grimm *et al.* 1996; Uchmánski & Grimm 1996). To keep up to other theoretical developments, it is also suggested that sub-models in IBMs should be standardized (Deangelis & Grimm 2014; Johnston *et al.* 2019).

In this work, we wish to use IBMs to generate theoretical advances regarding how species' populations may react to climate change. It is important to explicitly account for demography for understanding the effect of climate change. Species may go extinct, adapt or move, and all those possibilities are deeply linked to demography (Piou & Prévost 2012; Fourcade *et al.* 2017). We need to understand population dynamics to predict extinction probabilities (Burger & Lynch 1995; Uchmánski 2000; Pease *et al.* 2013); adaptation is also dependent on demography, as it is the result of population genetics and exchange of genetic diversity by individuals (Guisan & Thuiller 2005; Lavergne *et al.* 2010; Gomulkiewicz & Houle 2013); and movement is dependent on dispersal, which depends on environmental exploitation and individuals perceiving of local conditions (Hoffmann & Sgrò 2011). As conclusion, evaluations of impacts of climate change should use population dynamics explicitly, but also following the guidelines for model building already discussed previously.

Population dynamics are, overall, affected by two types of regulation: 1) intrinsic regulation, dictated by reproductive and growth capabilities and density-dependent regulation and 2) extrinsic factors, such as resources availability or harsh environmental conditions (Sibly *et al.* 2002). We chose to build the model rooted on two theoretical bodies we believe are the most adequate for the question: thermal ecology, as the effect of temperature is crucial for predicting climate change effects, and Dynamic Energy Budgets DEB theory (Nisbet *et al.* 2000; van der Meer 2006), a mechanistic theory relating organisms' size and development to resources usage, that has already been suggested and applied for IBMs (Deangelis & Grimm 2014; Beaudouin *et al.* 2015; Arnould-Pétré *et al.* 2021). As shown in chapter 1, thermal ecology is highly developed field, both in practical and theoretical grounds, and therefore should be able to sustain this model and grant communication to other models and empirical approaches. DEB theory is a highly tested framework, that has also been applied and validated in various IBMs (Alver & Hagiwara 2007; Martin *et al.* 2013; Beaudouin *et al.* 2015; Smallegange *et al.* 2016; Arnould-Pétré *et al.* 2021). In DEB theory, metabolism and physiological functions are predicted by organismal rules of energy allocation. Organisms allocate their energy reserves constantly for two types of processes: 1) somatic processes, which are somatic maintenance and structure growth or 2) reproductive process, which can be maturation, maturation maintenance and reproduction, according to the life stage of organisms. According to the theory, maintenance costs are priority to the organisms, and this energy allocation rules dictate how organisms' life history happens. One of the most interesting aspects of DEB theory is that body sizes emerge from how assimilation rates and maintenance costs of individuals escalate to body size, as assimilation capacity escalates to body surface, while maintenance escalates to body volume. DEB theory has the potential to integrate life history aspects and relate them to environmental resources, and thus it fits well to our need to use a consistent sub-model for populations' self-regulation. It allows us to use a small number of parameters and generate emergent density-dependent regulation and body sizes. It communicates well to other models, fitting on the idea of standardization of sub-models. The consistency and simplicity granted by DEB theory allows us to add realism and complexity to other parts of the model, and integrating this framework to thermal ecology theory in a multi-species approach can be viable. A lot of IBMs (some using DEB theory) are published in the literature, but even when they propose a more theoretical question (Travis *et al.* 1998; Wang & Grimm 2007; Dytham *et al.* 2014; Thierry *et al.* 2014; Malishev & Kearney 2017), they are usually oriented to a single species and therefore lack generality. The lack of a paradigmatic and general IBM for population dynamics is a challenge we wish to overcome in this study.

My objective in this chapter is to develop an individual-based model, rooted on energetic budgets and thermal performance curves to explore population dynamics emergent properties from those theories. Both thermal ecology and energy budget theories have been applied to higher biological organization levels, but an explorative approach on their consequences for population dynamics is still lacking. Instead of building highly detailed models for a given species, as has usually been performed, I want to explore how those solid based theories can be applied as tools for generating random species, in this case, of ectotherms, sustaining a more paradigmatic and general approach for population ecology. With the model, I intend on generating predictions about 1) how the coupling of those theoretical fields relate to some assumptions and generalizations common on ecology (e.g. growth patterns, thermal performance curves for different processes) 2) evaluate the predicted distribution of some population ecology statistics, such as developmental and reproductive rates and body sizes, and understand how these distributions may be dependent on environmental temperature or species' characteristics and 3) to evaluate how temperature affects patterns of abundance and fluctuation in species with different characteristics and body sizes.

Methods

We are following a protocol specifically build for describing IBMs, the ODD protocol (Grimm *et al.* 2006, 2010).

OVERVIEW

Purpose

Our purpose is to generate predictions on population ecology and abundance patterns of species based on concepts from thermal ecology and ecophysiology (DEB theory). Usually, population ecology is approached in a very specific way; models are developed and parameterized for species, and results are validated with independent populational data sets. We are using an opposite approach: we intend on generating a variety of random ectothermic species with different life histories and thermal sensitivities, in order to explore how patterns of population dynamics can emerge from different species and their nature. Life history, as well as some demographic processes (density dependent regulation) will be based on DEB theory, a consistent framework that has already been validated for various species in individual and population levels (Van Haren & Kooijman 1993; Bacher & Gangnery 2006; Kooijman *et al.* 2008; Martin *et al.* 2012; van der Meer *et al.* 2014). The performance of individuals in different temperature regimes will be modeled using some of the theoretical advances made in thermal ecology. In this framework, the life history and population characteristics from the species will emerge from the interaction of energy budgets and the thermal sensitivity of the species. Species with different body sizes will emerge from differences on physiological parameters (because ingestion capacity increases with organisms' surface, but maintenance energy increases with organisms' volume), and temperature will modulate the timing and viability of the populations in different regimes. If our results are consistent and realistic, this simplified model should also serve as a basal framework for the other chapters of this thesis, which should incorporate microevolutionary dynamics.

To explore the models' predictions, we will evaluate 1) concordance with some other patterns expected for individual life histories and population dynamics, 2) the distribution of individual rates in the populations (development and growth rate, fitness, or realized fecundity) and how they change on more extreme temperature regimes and 3) evaluate how body size and environment (difference from optimum temperature and temperature variability) affect population statistics.

Entities, Attributes and Scales

The model accounts for individuals and the environment and runs on a daily scale (table 1). Individuals are organisms of a random generated species, and are characterized by their body size, age, sex, life stage (egg, juvenile or adult), gonotrophic cycle, and energetic state (energy accumulated in reserves and gonads). Species are characterized by their energy allocation strategy (kappa value) and energetic parameters (ingestion capacity and maintenance/growth energetic costs). The environment is characterized by the temperature regime (monthly means of fixed or variable temperatures) and food availability (a daily fixed production of food portions and their energetic contents). The model has no spatial structure, and assumes a population isolated from other species with no emigration/dispersion.

Table 1: Entities, their attributes, and their values or assumed relationships. Entities are separated as the environment, species, and individuals. In species, attributes are separated in parameters or values allometrically assumed. For individuals, the values of the attributes are dynamic and * means they may vary on a daily basis.

Entity	Variables/Parameters	Functioning	Values
Environment			
	Resources	A vector representing food portions obtainable by the individuals.	2000 portions generated each day, containing a maximum of 900 energy units each.

Entity	Variables/Parameters	Functioning	Values
	Temperature regime	The environmental temperature, that causes the body temperature to function by its' value.	Consists of monthly means, in fixed or variating scenarios (figure 4).
Species	**Parameters** (Values are fixed for individuals of the same species)		
	Ingestion capacity	The potential feeding capacity of the species. Its' a rate, related to the organisms' body surface. Measured in energy units/cm².	Ranges from 50 to 400.
	K-value	A value ranging from 0.5 to 1. Represents the energy expenditure strategy. Mobilized reserves is used on somatic (multiplied to K) or reproductive functions (multipied to 1-K).	Ranges from 0.5 to 0.9.
	Maintenance cost	The cost needed to maintain 1cm³ of structure alive and non-damaged. Measured in energy units/cm³.	Ranges from 15 to 20.
	Growth cost	The cost needed to generate 1cm³ of structure.	Ranges from 400 to 2600.
	Derivated values (calculated allometrically)		
	Maximum size	The size reached by individuals in a food abundance scenario. Emerges from the interaction of the species' parameters.	Emerges from the interaction of the species' parameters.
	Maturation threshold	Juveniles spend reproductive energy (1-k of mobilized reserves) on maturation. As this accumulated energy reaches this absolute threshold, juveniles become adults.	Assumed as the energy needed to grow 1% of maximum size.
	Maturation maintenance	The cost needed to maintain reproductive tissue functioning.	Very small value calculated allometrically as 30x1% of maximum size.

Entity	Variables/Parameters	Functioning	Values
	Energy contained in an egg	Eggs are individuals with no relevant structure and large amounts of reserves. Those reserves come directly from its' progenitors' gonads accumulations.	Assumed as the energy needed to grow 2% of maximum size.
	Gonotrophic cycle duration	The time needed for a female to produce eggs. It lays eggs in the end of each cycle. It is measured in days.	Calculated through an assumed allometric equation. Assumed as 1 additional day for each 8.5 cm³ of volume.
Individuals			
	Age	Age of the individual, measured in days.	*
	Structure	Organisms' body size, measured in cm³.	*
	Reserves	The amount of energy accumulated in reserves (blood molecules/fat). Measured in a given energy unit called "energy units".	*
	Stage	Life stage, as egg, juvenile or adult.	*
	Maturation	Energy accumulated for maturation process. It is the process of developing tissue and organs for sexual finalities. Juveniles become adults when this accumulation reaches a threshold.	*
	Gonotrophic cycle development	Days passed in the current gonotrophic cycle. Females lay eggs when this value equals to the cycle duration, and this value returns to 0.	*
	Gonad energy	For adults only, it is the energy accumulated in reproductive organs. It is used for generating eggs in females. Measured in energy units.	*

Process overview and scheduling

At the beginning of each day, several food portions are generated in the environment. Those food portions, characterized by their obtainable energetic content, are randomly acquired by different individuals. These portions represent resources the species can use, and for simplicity their energetic values already incorporate losses due to digestion efficiency and costs of food searching and manipulation. Individuals then assimilate that energy into their reserves, limited to a daily maximum given by the organisms' surface. The amount of food portions available and their energetic contents are fixed, and so this works as a density dependent regulation factor. Thus, higher individual numbers cause lack of food portions for some individuals. After the assimilation (incorporation of energy from feeding on individuals' reserves) the model runs the reserves dynamics, which mobilizes some of the reserves (an amount given by a parameter called conductance) and allocates them to different physiological processes according to what has been proposed by DEB theory. After this allocation, the model checks if there are female individuals ready for reproduction. Adult females which complete their gonotrophic cycles in this day lay eggs according to the reserves accumulated in their gonads, and those eggs are added to the population randomized as male or female with equal chance. After reproduction occurs, the model checks individuals that either overcome their longevity or did not have enough energy to sustain their maintenance cost for the day, and those are considered dead and removed from the system. The algorithm gets some statistics from the populations, according to the analysis required, and then the daily cycle is completed and starts over again. An overview of processes can be seen in figure 1, alongside with and overview of an organisms' life history as it happens in the model.

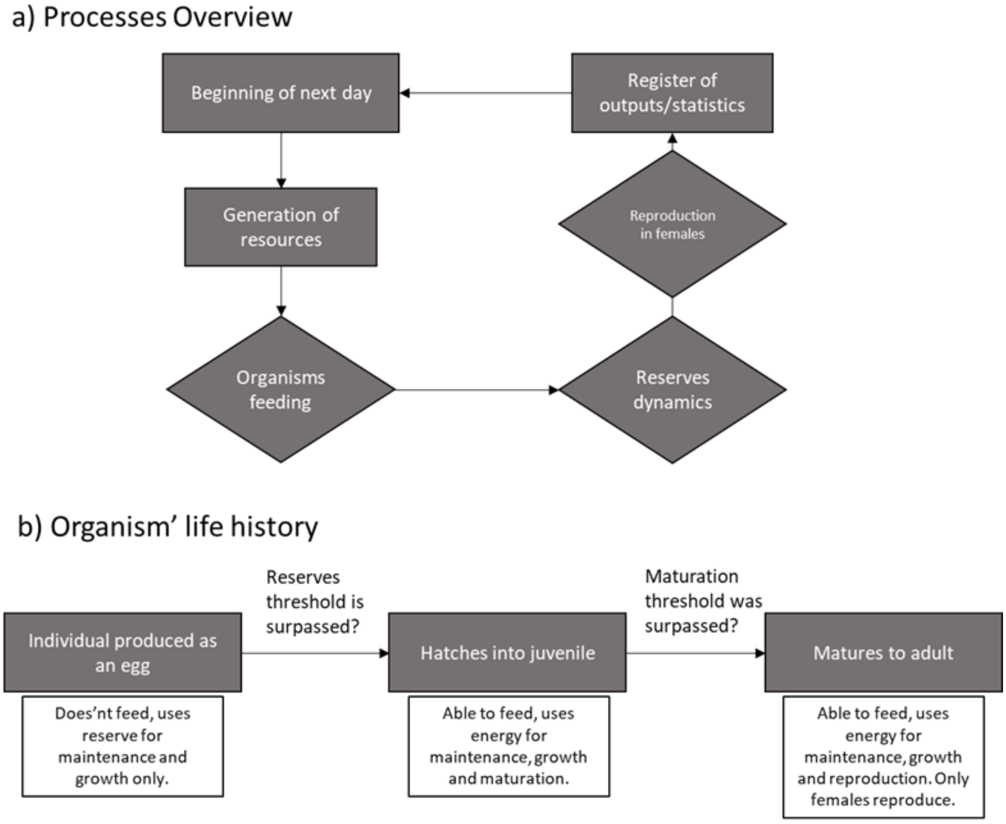

Figure 1: a) an overview of the models' processes in the daily cycle. b) life processes that happen though an individuals' life history. Thresholds dictate how individuals change life stages, and life stages dictate individuals' feeding ability and reproductive energy (1-k) usage.

DESIGN CONCEPTS

Basic principles

The model is based on the idea that the population properties and dynamics emerge from resources availability interacting with the way individuals apply energy for life processes and different efficiencies for those processes at different temperatures. The most important principle of this model is probably the kappa rule, a very important component from DEB Theory that we are borrowing. This assumption states that energy allocation for different organs and functions of the body is overall proportionally constant, because this energy expenditures are related to reserves density in the blood and diffusion through the organism. Therefore, energy is invested in somatic or reproductive processes in a constant rate dictated by the kappa value (k for somatic processes, 1-k for reproductive processes) through all of an organism's life history (cite), with eggs being the only exception. We assume that some details of the energetic expenditures of the organisms depend on their life stage. Eggs are unable to obtain more energy through feeding and do not use energy for reproductive finalities; juveniles are able to feed, and use energy for reproductive finalities in the form of sexual maturation; adults are also able to feed, and use energy for reproduction in the form of maturity maintenance and egg production. Those changes in the profile of energetic budgets modulate how the life history of the species happen (figure 1b). The model also accounts implicitly for density dependent regulation through resources availability, as the daily production of resources is constant.

Another important component of the model design is the effect of temperature on life processes. We know extensively that enzymatic activity is highly dependent on temperature, because of activation energy and stabilization of their physical structures (Somero 1995; Fields 2001). We incorporated this effect in the form of limitations in the effectiveness of energy expenditure. Unfavorable temperatures reduce the amount of energy obtained from ingestion (because of more difficulties on food handling or digestion) and increase both maintenance and growth costs (because the organism must spend more energy to cope with the physiological costs of harsh temperatures, for example on processes that repair cellular and protein structure). Organisms in unfavorable temperatures will obtain less energy from the same amount of food, will spend more energy on maintenance and get lower growth rates. We also assume that the intensity of the effect is stronger for unfavorable hot temperatures, as it is proved that critical thermal maxima are overall less variable and that overheating is more prejudicial to the organisms than cooling (Araújo *et al.* 2013).

There are some assumptions we needed to take in order to make the model more tractable. First, we assume that the consumption of resources by the species has no effect on future resources generation. This assumption is unrealistic because consumption/predation usually reduces the resources' productivity. Incorporating more realism to this process would demand sub models and more parameters related to how the resources is affected by consumption, and we considered that this complexity would not be productive for our main questions. We also decided to simplify the environment, using monthly means and assuming that the organisms are uncapable of thermoregulation behaviors. We assume that all the species have the same temperature optimum and performance curves. In order to compare differences between species with different optimum and performance curves, we would need more assumptions on how curves are different, for example assuming different constraints and trade-offs in the curves' shapes (Huey & Kingsolver 1989, 1993). This would be a very interesting evaluation, but think we need a solid understanding of the models' dynamics before delving into those questions. We also assume that there is no intra-specific variation in DEB parameters, so that their effects could be more easily isolated in the results. We also assume a closed system, in which species are not affect by interactions with other species (by predation or competition) and populations (migrations). The model structure and algorithm were built in a manner that easily allows for incorporation of more sub models and complexity. Therefore, we do not see our simplifications and assumptions as just limitations, but also as opportunities for further exploration in future works.

Emergence

The species’ body size will emerge especially from the physiological parameters. An organisms’ maximum body size is limited by its’ maintenance cost (related to volume), because of ingestions’ incapacity (related to area) to surpass those needs at some point of its’ life. Population dynamics and properties will emerge from the allocation strategy of the species and its interaction with the efficiency rates given by environmental temperature. Individuals’ growth rates, reproduction rates (or fitness) and death chance will also emerge from this scenario, and probably dictate population dynamics on a higher level. The organisms’ life history will also emerge from the interaction of energy budgets and how they change depending on life stage. This allows us to compare the results with predictions from classical theories and other models, and evaluate the models’ realism, but also allows our model to generate counter-intuitive results that might be interesting for the moment.

Stochasticity

Stochasticity is present in the resource’s “distribution”. A number of food portions is generated on the environment each day, each of them with a random energy content up to 900 energy units and is randomly distributed to the organisms. This causes some individuals to be able to grow and reproduce, while others will not. All other processes are deterministic, and almost all stochasticity in our results (variations in body sizes, reproductive rates, population fluctuations) are results of this random feeding process. For the model analysis, we also used a random process for generating the species. We generated 100 random species, meaning that they have random energetic parameters (ingestion coefficient, maintenance energy, growth energy and the kappa value) according to what is described in the initialization section. This is also a source for variation in the results, but is not a random process inside the dynamics per se.

DETAILS

Initialization

In order to analyze our model, we created 100 random species with different values for the energy budget parameters (ingestion coefficient, maintenance and growth costs and the kappa value) ranging from the values listed on table 1. After that, those inputs are used in a sub-model to generate the species maximum possible body size. This sub-model containing an individual egg in food abundance is run for enough time for that individual to reach its' maximum potential size. This maximum size is obtained through some of the energy budget parameters (the ingestion coefficient, maintenance cost and growth cost). The ingestion coefficient is a constant that multiplies body surface (cm^2), and maintenance costs multiplies the body volume (cm^3). Because of this, organisms get to a moment in which all of their somatic expenditures must be invested on maintenance, because ingestion cannot grow more to accommodate more growth. The maximum potential size of the species is used to calculate some allometric parameters that will matter for the organisms' life history. Those allometric parameters are: energetic threshold for sexual maturation or becoming an adult (1% of the energy needed to generate 1% of the maximum structure), the value of reserves contained in each egg (2% of the energy needed to generate 1% of the maximum structure) and the duration of the gonotrophic cycles (according to the equation present in table 1). We used those species for some isolation runs (runs of a single individual, through its whole lifespan, in order to analyze potential growth and reproduction in resources abundance) and some population runs (runs of whole populations, that allow evaluation of population dynamics) on different temperature scenarios (figure 2). The population runs started as 40 individuals (20 for each sex), with state variables randomized inside the range of what is possible for the species (random sizes, reserve quantities, age etc.) and occurred through a period of 15 years.

Observation, Input data and Analysis

At each day, we observe the number of individuals in the population, and in the end of the run we compute statistics such as mean growth and reproduction rates, as well as body size distributions and population measurements (mean and standard deviation of the number of individuals throughout those years).

The input data for the model are simply the species energetic parameters (figure 2) and the environmental data (resources and temperature). The energetic parameters are randomly generated for 100 species, as we already exposed. The food or resources are composed of a daily production of 2000 "portions" of food, each containing a random amount of obtainable energy up to 900 units. For the temperature, we did not incorporate absolute values, but values relative to the species optimum. We consider two types of scenarios: fixed temperatures throughout a year (which is not a realistic scenario, but is theoretically useful for understanding the effect of temperature variability) and monthly means variating up to 4 total degrees (+2 and -2 relative to the species optimum). For both cases (fixed and variating regimes) we also applied scenarios of more unfavorable climates, which we incorporated as a summation to all monthly temperatures, ranging from -6 to +5 degrees. A simplified visualization of those regimes can be seen in figure 3.

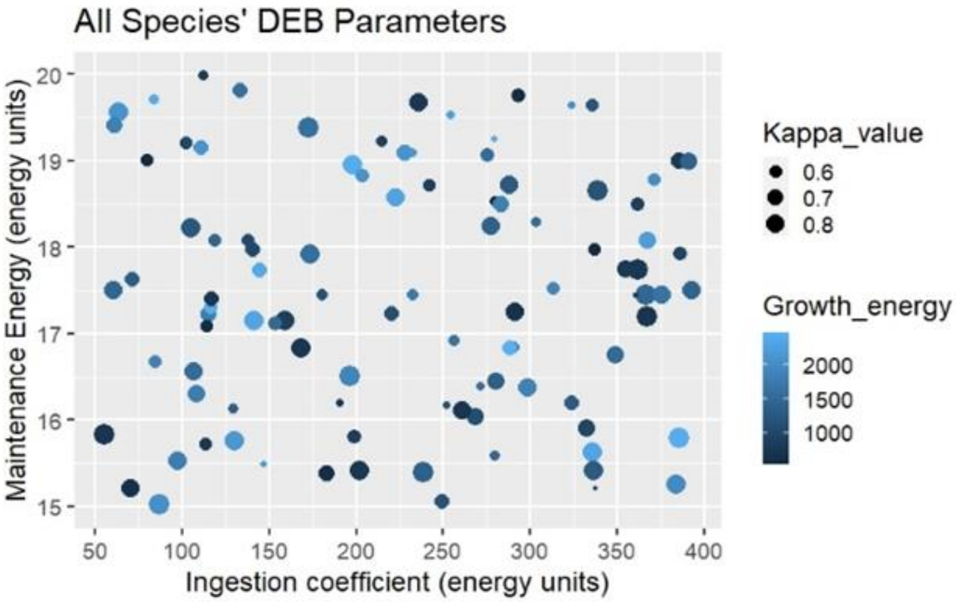

Figure 3: The energetic parameters (maintenance energy, ingestion capacity, kappa value and growth energy) of the 100 species used for models' analysis. Those parameters were randomly generated, with a uniform distribution.

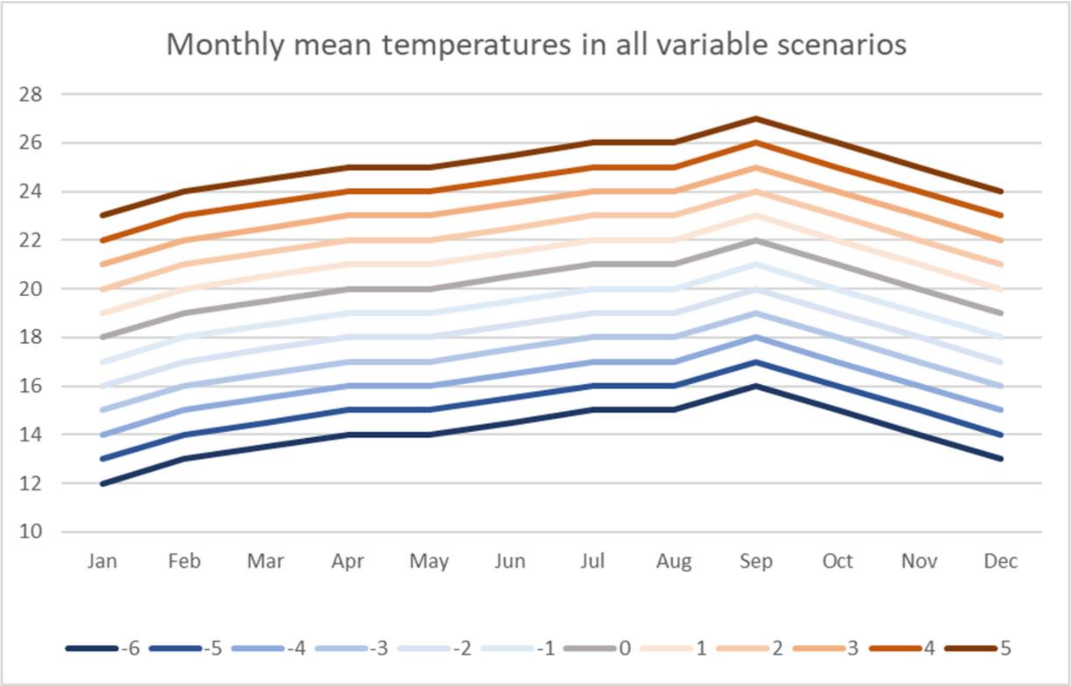

Figure 4: the temperature scenarios for inputs of the model. A "neutral" scenario (grey line, 0 change) with mean of 20º Celsius and variation of 4 total degrees (ranging from 18 to 22) is used for generating change scenarios ranging from +5 mean degrees to -6 mean degrees. For fixed scenarios, temperatures are the same for all months, ranging from 14º Celsius to 25º Celsius.

Regarding the analysis, at first, we will analyze results of single individual runs, representing a “laboratorial experiment” of maximal food availability. This is useful for comparisons with population scenarios and discussing how the populations will regulate themselves. We will record the maximum size, growth rate and reproductive rate of single individuals, in different fixed temperature scenarios (ranging from -6 to +5 degrees relative to the optimum) and relate them to the energetic parameters of the species. Regarding runs based on populations, we will track 1) mean and variation of abundance, 2) mean and variation of reproductive rates and 3) mean and variation of body sizes throughout the fixed and variable temperature scenarios described above. We chose to calculate those statistics for 12 years, ignoring the first three years of the model run, in order to avoid bias by transient initial states.

Of the 100 species, only 71 were viable, meaning that 29 species were unable to maintain populations even in optimal temperature scenarios. We conducted a logistic regression to understand is species’ viability is related to body size and the species’ parameters. We will use two metrics of body size (maximum body size in isolation and food abundance and mean body size in population runs) and the energetic parameters as predictors of populations statistics (mean and standard variation of abundance). We also used temperature change scenarios as predictors to those population statistics. Species displayed different shapes for the relationships between temperature change scenario and abundance, and to analyze this effect we fitted the relationship of each species to a quadratic equation ($y=a+bx+cx^2$). After that, we used the energetic parameters to understand if the differences between those shapes can be systematically predicted, using the coefficients from the quadratic equations as response variables.

SUB-MODELS

Foraging

At the beginning of each day, a number of 2000 obtainable resources patches (food) are generated. Those patches, or portions, have a random energetic content, randomly variating from 2 to 900 energy units. This energetic content already assumes energy costs on handling and searching food, and also the losses by digestion efficiency. Those resource portions are randomly designated to different individuals in the population. This food distribution process is not uniformly random, as we incorporated a higher probability or getting a portion for larger individuals by separating a fraction of the resources for those individuals. It is reasonable to assume that larger individuals are competitively superior in resources acquisition, because they should display features like more movement, a greater surrounding area for searching and sensing and because they would also win direct confrontations. This feature can have an important effect on population dynamics (Roos & Persson 2003; Smallegange *et al.* 2016), because it changes the form of how competition works.

Energetic dynamics

After an individual assimilated energy from a resource patch, that amount of energy is directly added to its' body reserves. After that, each day, reserves are mobilized to physiological functioning through the sub model of reserves dynamics (figure 3). A fraction of the reserves' content, defined by the parameter energy conductance (a 0.5 value fixed for all species) if used/mobilized. This energy conductance parameter is necessary, because the distribution of energetic compounds to tissues is performed by chemical diffusion, and therefore in large reserves scenarios it could not be totally used in a single day. That mobilized reserve is used to growth and maintenance in eggs, and for two different finalities in juveniles and adults: somatic and reproductive efforts. The division of energy allocated to somatic or reproductive functions is defined by the parameter k, the kappa-value.

Regarding somatic functions, maintenance has a priority factor over growth. This means that organisms would never allocate energy to growth if their maintenance costs were not fully contemplated. Individuals which are unable to dedicate all energy required by their somatic maintenance are considered dead by starvation. The maintenance cost is calculated by the multiplication of the species' energy maintenance parameter (measured in energy units/cm^3 of volume) to the organisms' volume. After the maintenance costs are applied, if there are still remnants of energy for somatic processes, that energy is used for structure growth. This process increases the organisms' size, by an amount calculated by the division of the energy remnants by the species' growth cost parameter (energy/cm^3, or the energy necessary to create $1cm^3$ of structure).

The organisms apply a proportional fraction of 1-k of their mobilized reserves to reproductive processes. This only happens in juveniles and adults. Juveniles apply that energy to a maturation buffer. Energy is accumulated to this buffer, and the organism becomes adult after it reaches a threshold (table 1). Adults use that energy for maturation maintenance and egg production. Similar to what happens in somatic processes, maturation maintenance also has priority. After the organism uses the energy to maturation maintenance, the energetic remnants are allocated to a buffer dedicated to egg production. This buffer will be converted to eggs after a female completes its gonotrophic cycle.

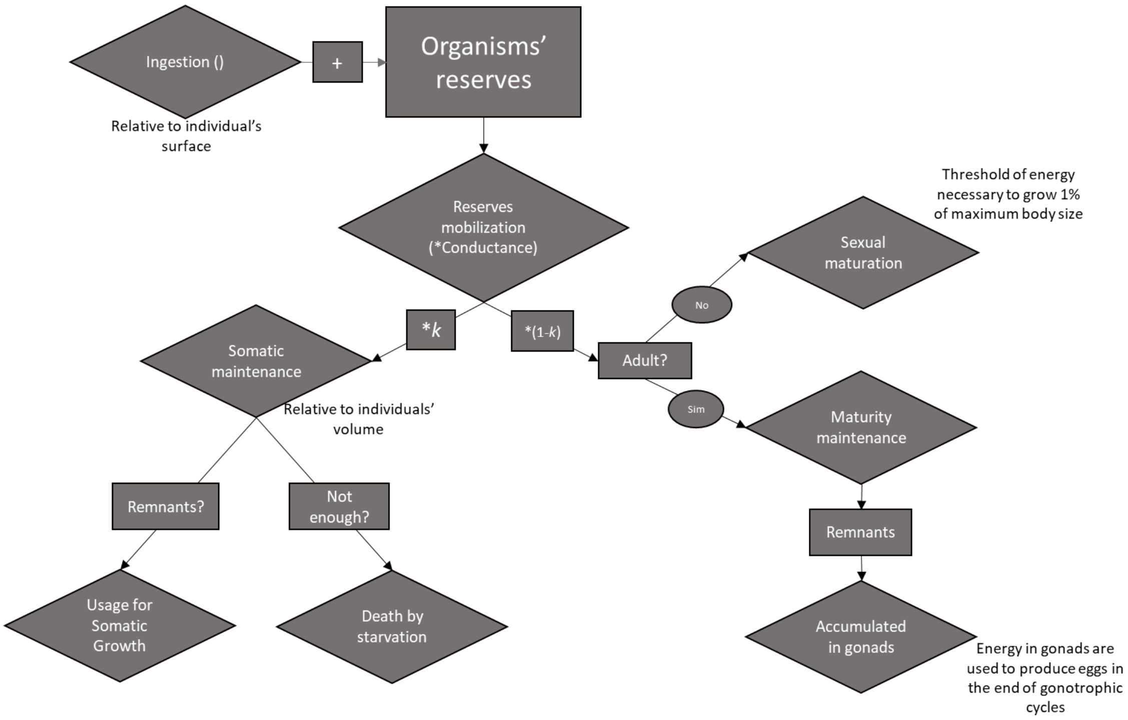

Figure 5: the reserves dynamics. Individuals go through the reserve's dynamics once each day, after the foraging sub model and the possibility of energy ingestion. Every day half of reserves is mobilized and spent into somatic (k) and reproductive (1-k) processes. In both somatic and reproductive processes, maintenance costs have priority over reproduction and growth. Reproductive processes are dependent on life stage.

Temperature effect

In our framework, temperature changes the effectiveness of physiological functions through modifying the efficiency of energy usage (Figure 4). Three processes are affected by temperature: somatic maintenance, growth, and ingestion. Differences from environmental temperature to the species' optimum cause maintenance costs to be higher and ingestion and growth efficiencies to be lower. We assume a linear pattern for the change in those efficiencies, and a steeper slope for hotter temperatures than for colder temperatures (slopes of 0.05 and 0.03, respectively).

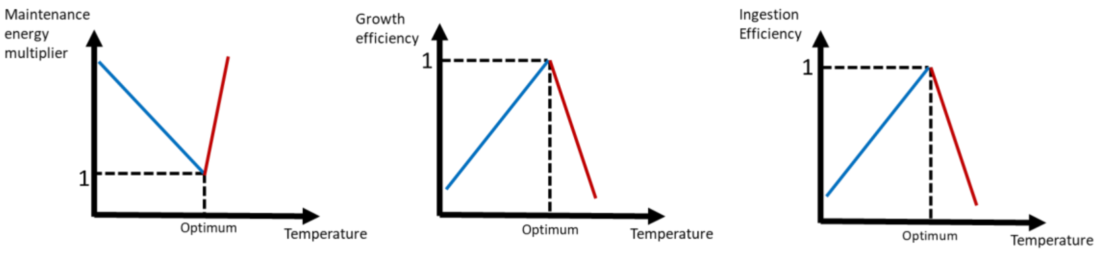

Figure 6: the effect of temperature on energy use efficiency. As environmental temperature is different from the species' optimum, the individuals 1) need more energy for somatic maintenance, 2) use energy less efficiently for growth and 3) assimilate less energy by ingestion. The slope of those relationships is different for hotter and colder temperatures, and have values of 0.5 and 0.3 respectively.

Results

We present the results in two perspectives: on isolated individuals, simulating laboratory conditions on food abundance and on populations. Simulations on isolated individuals demonstrated that the model seems to follow some well-established patterns related to individual functioning. Individuals and present intuitive performance curves when whole-organism processes (growth and reproductive rates) are examined on fixed temperatures (figure 9). An interesting emergence for the performance curves of whole-organism processes is that they display slightly nonlinear performance decrease, even though the sensibility of the physiological functions was modeled as a linear effect. The growth rate displayed a positive relationship with body size, and offspring number displayed a bell-shaped relationship with body size, in which species with intermediary body sizes display larger offspring numbers (figure 8). We expected this positive relationship for growth rate, but that relationship for offspring number is counter-intuitive, as we expect from ecological theory that smaller species should have the higher offspring numbers.

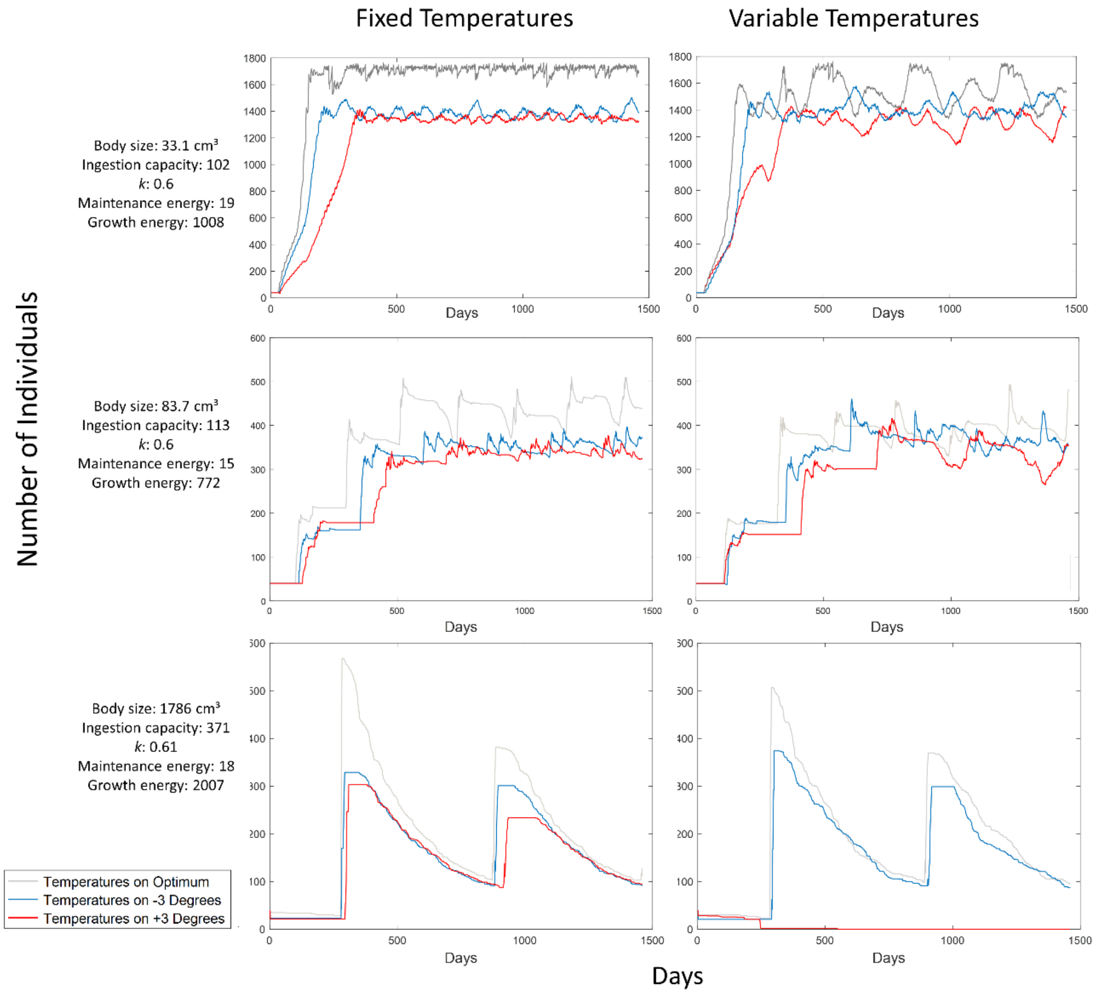

Figure 7: runs of three different species for exemplifications of the generated system. Graphs show population dynamics of 3 species with different parameters and body sizes under 5 years of model run for fixed (left) and variable (right) temperature scenarios on optimum (grey lines), +3 (red lines) and -3 (blue lines) temperature changes.

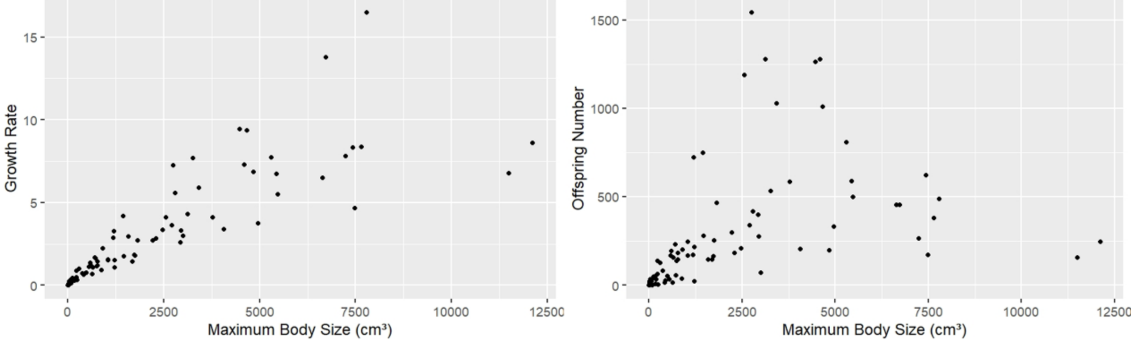

Figure 8: results from single individuals in food abundance scenarios. Growth and reproductive rates are correlated to maximum body size of the species.

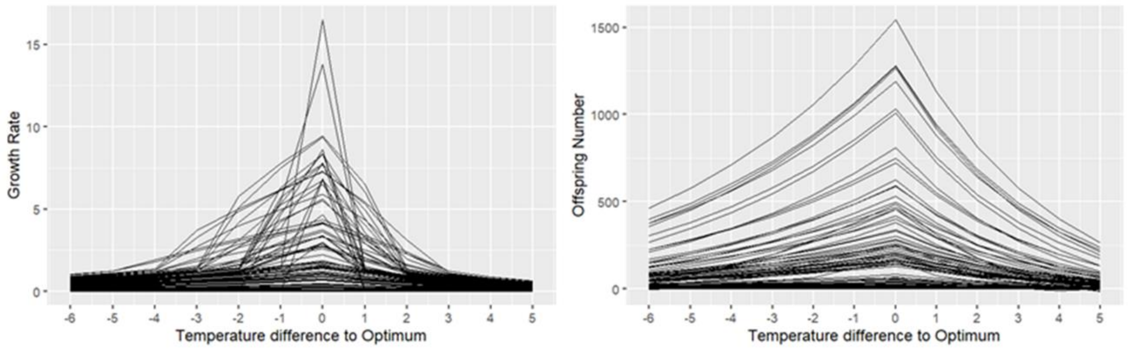

Figure 9: Growth rate and offspring number per female on isolation and fixed temperature scenarios ranging from -6º Celsius to +5º Celsius relative to species' optimum.

The relationships between the energetic parameters and body size metrics follow what could be predicted from DEB theory (figure 10). Three parameters affect body size: ingestion capacity, maintenance energy and the kappa-value. Body size is negatively related to maintenance energy and positively related to ingestion capacity and the kappa-value. Those patterns are the same for the maximum body size and for mean body size on populations. Mean body sizes on populations were small compared to the maximum values those species could obtain (figure 10), suggesting that competition leads to lower resource levels and consequently body sizes. Body size was also correlated to population statistics, causing lower mean population numbers and more stable populations (figure 11).

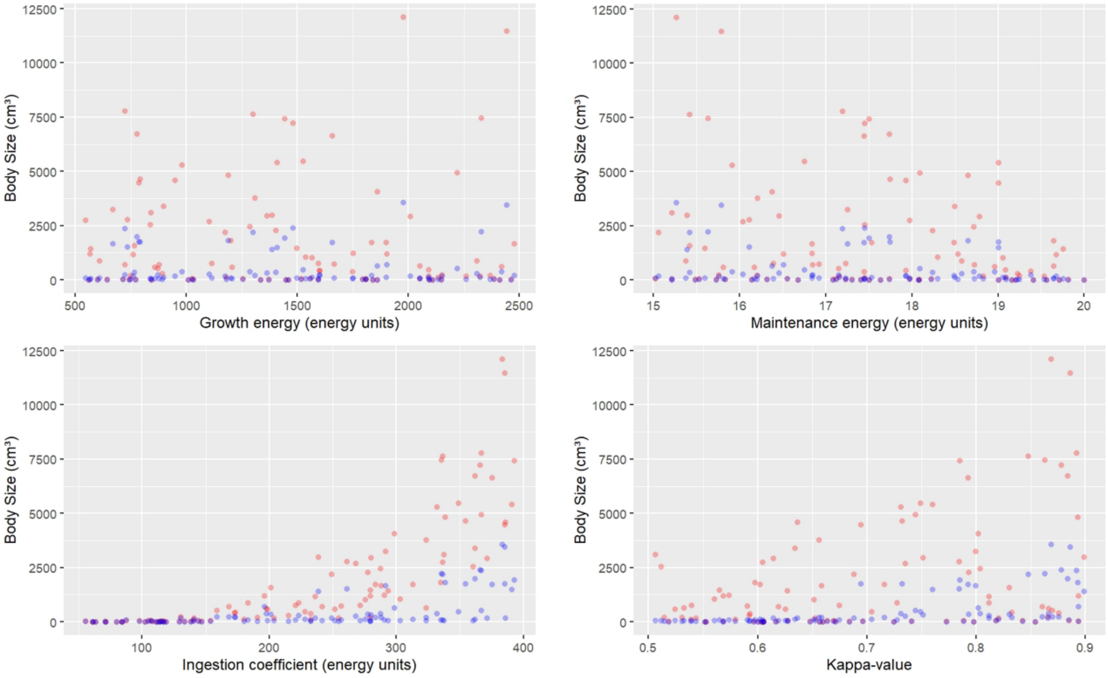

Figure 10: Relationships between the energetic parameters and organisms' body size. Red points indicate bod size in isolation and food abundance scenario, blue points indicate populational scenarios that incorporate competition. Ingestion capacity, maintenance energy and the kappa value are correlated to the body sizes.

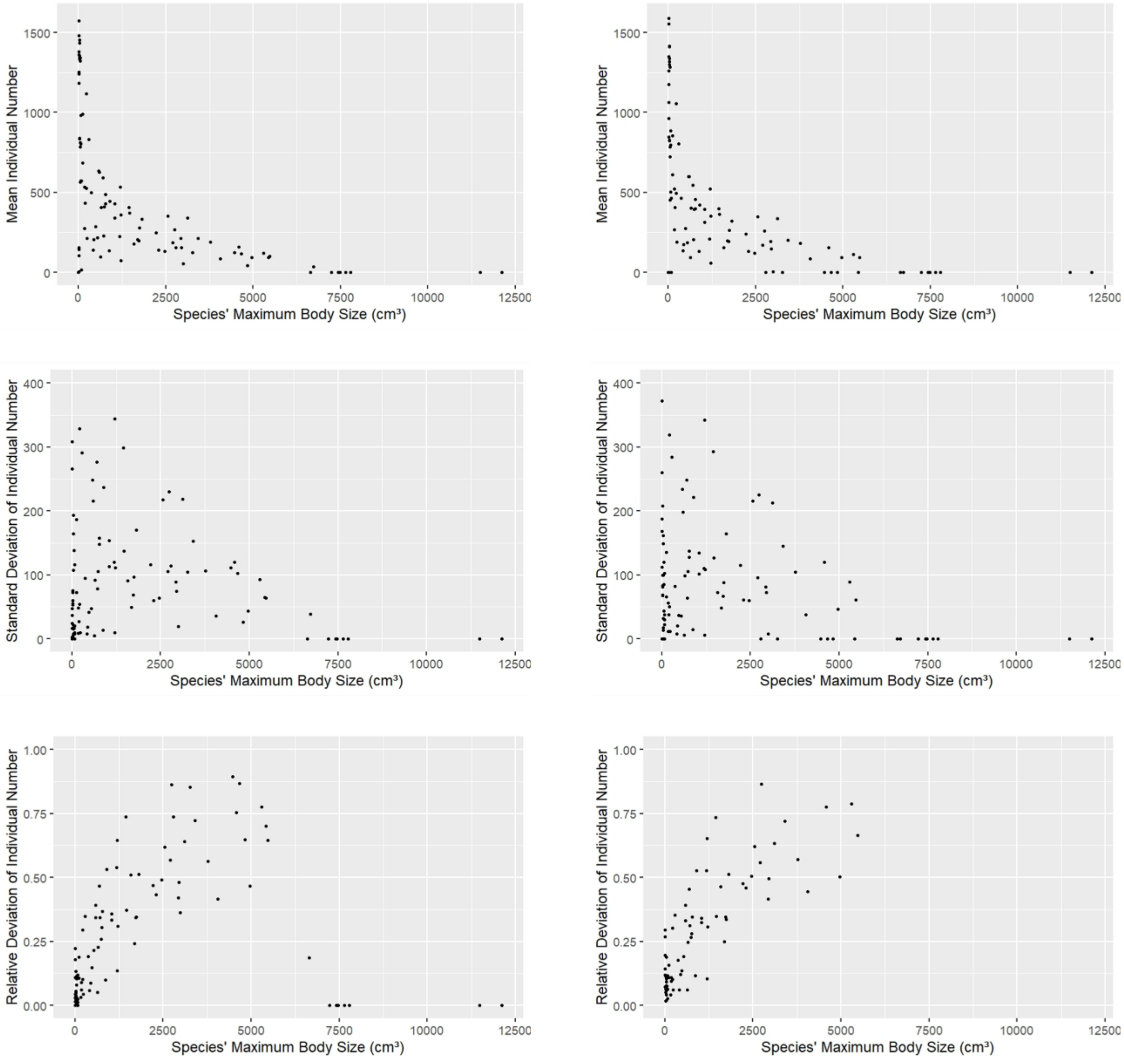

Figure 11: Mean and standard variation of abundance for species run in fixed (left) and variable (right) temperature regimes. Species with larger body sizes lead to lower and less stable abundance patterns.

We were also able to understand the effects of the energetic parameters on population statistics directly through regressions and quantile regressions (figure 12). We would assume at first that this should be true, because if energetic parameters predict body sizes, and body sizes predict the population parameters, a similar relationship should be expected. As such, the parameters which increase body size (ingestion capacity and the kappa-value) had a negative effect on mean and standard deviation of abundance, but maintenance energy (which decreases body size) had a very small or null effect on abundance. A new feature appearing here is that growth energy, which does not affect body sizes, affects populations dynamics, negatively related to mean and standard deviation in abundance. Growth energy was positively related to mean and variation of body sizes, and therefore affects body size in populations, differently to maximum body sizes in isolation.

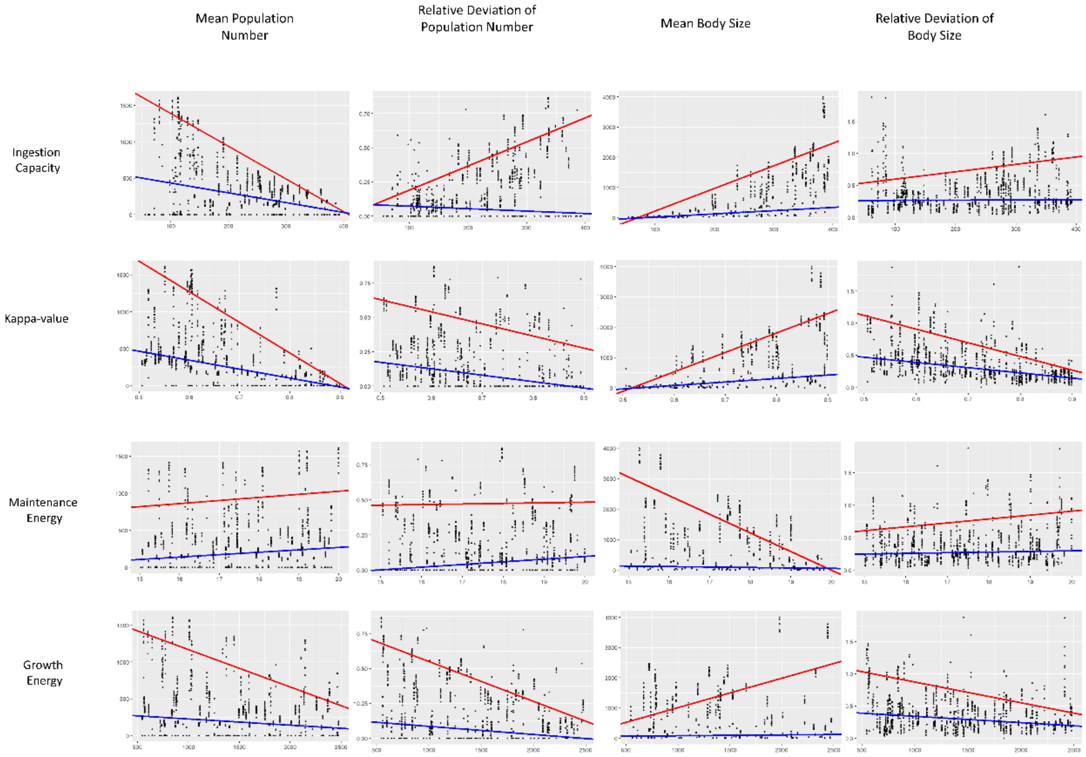

Figure 12: Regressions (blue line) and upper 90% quantile regressions (red line) of the effect of energetic parameters on populations properties.

Of the 100 randomly generated species, only 71 were viable, meaning that 29 were not able to maintain populations in competition scenarios. This viability had a strong negative relationship with body size ($p<0.001$, figure 13 and table 2). The extinct species also display a profile of energetic parameters, being of species with too low or too high ingestion coefficients coupled with high kappa-values (figure 13).

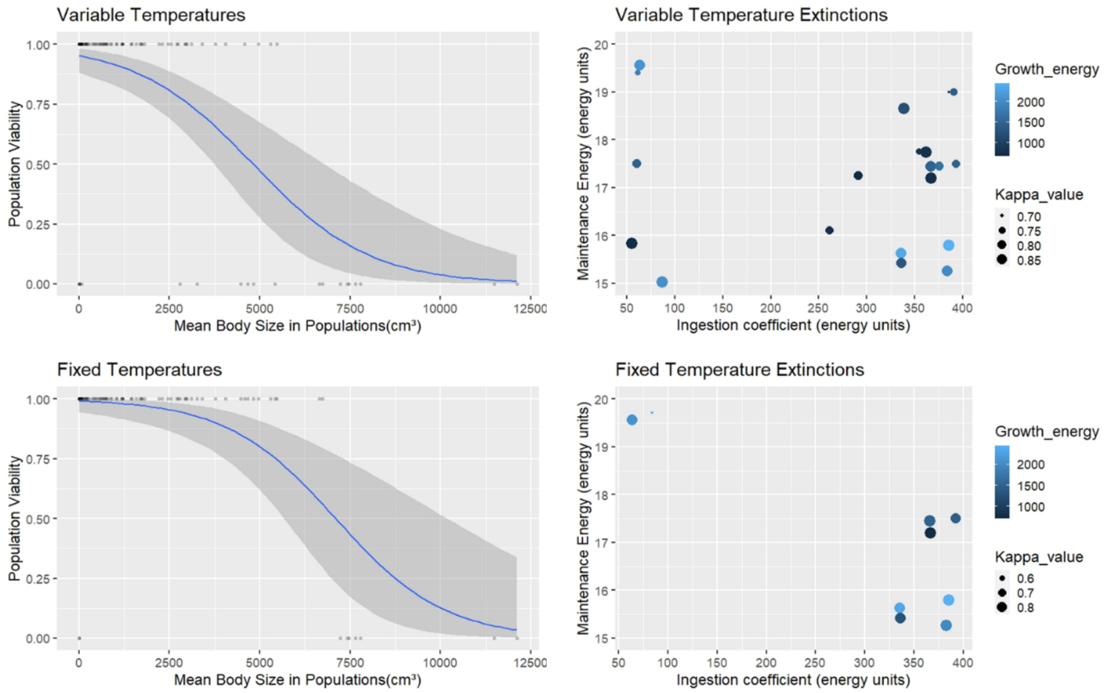

Figure 13: logistic regression model of population viability (capacity of avoiding extinction on competition scenarios) and the energetic parameters of the not viable species. Viability is related to body size and energetic parameters.

Table 2: logistic regression results. Extinction of populations on optimum scenarios is predicted by maximum body size of the species.

	Population Viability by Body Size			
Fixed Temperatures				
	Estimate	Std. Error	z value	P value
Intercept	4.72	0.959	4.921	<0.0001
Maximum Body Size	-0.0006	0.0001	-3.796	<0.0001
Variable Temperatures				
	Estimate	Std. Error	z value	P value
Intercept	2.989	0.504	5.924	<0.0001
Maximum Body Size	-0.0006	0.0001	-4.541	<0.0001

Regarding the effect of temperature, it is simple in a general point of view but complex when looking at how each species responds individually. By plotting the means of abundance mean and standard variation for each temperature scenario, a predictable pattern of abundance decrease emerges (figure 14). It is a surprising fact that maximum abundance occurs not only on optimal temperatures but also on slightly suboptimal temperatures (there is no difference from 0 and -1 change scenarios). Standard variation follows the same pattern of means, but this is probably due to the fact that the two variables are correlated. I must build a dataset with relative variations to analyze variation per se. Our model predicted that mean body sizes increase on warmer temperatures (figure 15).

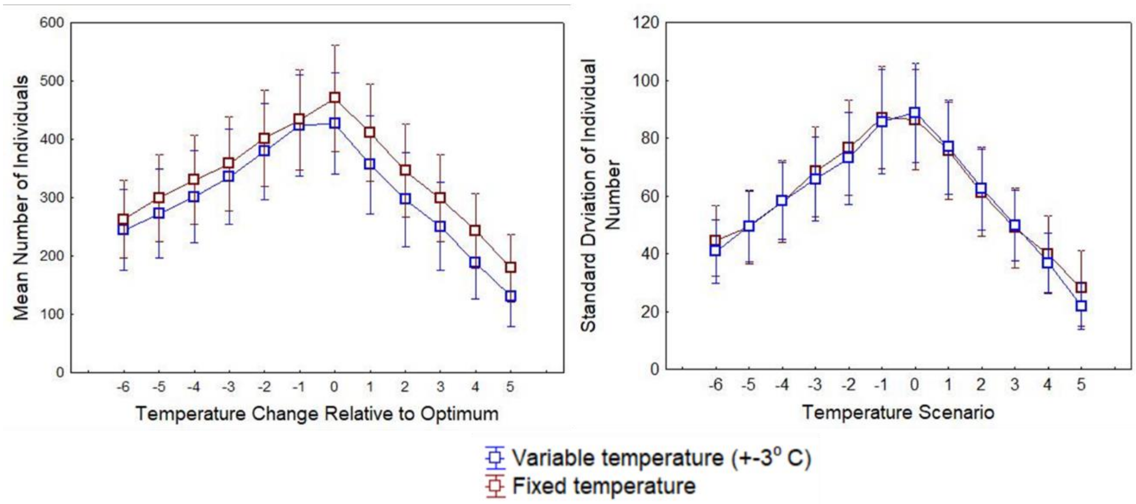

Figure 14: Overall effect of temperature on abundance for all species. Means of populations mean and standard deviation numbers are related to the scenarios of variable temperatures. the 100 species means and confidence intervals are presented.

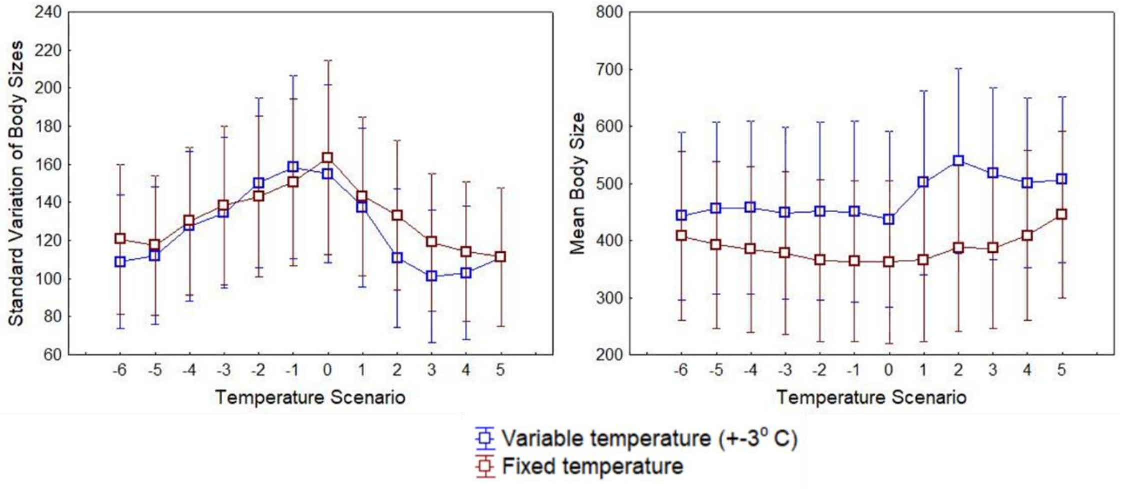

Figure 15: Overall effect of temperature on body size for all species. Means of populations mean and standard deviation of body sizes are related to the scenarios of variable temperatures. Graph shows means and 95% confidence intervals.

The energetic parameters influenced the shape of the temperature-abundance relationship (table 3). No parameters significantly affect the static coefficient, as would be predicted because this coefficient shapes the “height” of the curve which is the same for all species because it was standardized. The linear and quadratic relationships are predicted by all parameters but maintenance energy. Ingestion capacity affects negatively the linear and quadratic coefficients, and the kappa-value and growth energy affect them positively. The ingestion negative effect on the quadratic coefficients suggest it makes the curves wider, thus causing a more generalist layout, and the opposite effect is true for the kappa-value and growth energy. As the analysis in figure 13 displayed a suboptimal peak for abundance, we also chose to conduct this analysis for the vertex of the quadratic equations, representing what would be the actual optimum for population parameters. This suboptimality was ubiquitous in species, as the vertex of the equations shows a value of -0.96 and a standard deviation of 0.24, and regression results show that this suboptimality is positively affected by ingestion capacity and the kappa-value.

Table 3: Multiple regression results. Energetic parameters are used to predict the coefficients and vertex of the temperature – relative abundance quadratic relationship.

Static coeffient (a)			
R-squared: 0.01	Estimate	t value	p value
Intercept	1.28	11.531	<0.0001
Ingestion capacity	0.0001	1.765	0.08
Maintenance Energy	-0.004	-1.057	0.29
Growth Energy	-0.00008	-0.815	0.41
Kappa-value	0.006	0.011	0.99
Linear coefficient(b)			
R-squared: 0.31	Estimate	t value	p value
Intercept	0.042	0.383	0.702
Ingestion capacity	-0.0003	-3.733	<0.001
Maintenance Energy	-0.004	-0.869	0.388
Growth Energy	-0.00002	2.26	<0.05
Kappa-value	-0.18	2.535	<0.05
Quadratic coefficient(c)			
R-squared: 0.15	Estimate	t value	p value
Intercept	0.02	0.307	0.75
Ingestion capacity	-0.0001	-3.441	<0.01
Maintenance Energy	-0.003	-1.226	0.22
Growth Energy	-0.00005	2.877	<0.01
Kappa-value	0.131	3.046	<0.01
Vertex			
R-squared: 0.17	Estimate	t value	p value
Intercept	-2.33	-1.22	0.22

Ingestion capacity	0.005	3.42	<0.01
Maintenance Energy	-0.13	-1.481	0.14
Growth Energy	0.0003	1.573	0.12
Kappa-value	3.12	2.484	<0.05

Discussion

The IBM we developed seems to realistically simulate some of the most important drivers of population dynamics. The model made possible to understand how energetic budgets and temperature might affect a higher level of biological organization, on a macroecological perspective of population dynamics. Some of our predictions are qualitatively close to the general expectations of our current ecological theory. Thermal performance curves for growth rate and reproductive rate were not linear, and qualitatively concordant to expectations. Although all species have the same thermal sensitivities and organismal processes, differences in the energetic parameters led to very contrasting population dynamics and abundance-temperature relationships, and the shape of the abundance-temperature relationships was dependent on species' body sizes and its' determinants. Overall, the model correctly incorporated DEB theory, as relationships between the energetic parameters and body size agree to their predictions, even when we incorporated only a fraction of the theories' parameters and processes. We generated macroecological relationships between body size and metrics of population dynamics, as mean abundance/carrying capacity decreased exponentially with body size and standard deviation of abundance/instability increased linearly with body size. It was also possible to predict what would be the viable combinations of DEB parameters, and therefore what could species' optimal strategies, based on an analysis of the viability of modeled populations. This last result, especially, could be very interesting for model validation and further validation of DEB theory.

The objective of this contribution was the development of a population model that could be useful for various species in a paradigmatic approach. However, even this initial exploration of the emergencies led us to important findings. At first, the reproductive output of different species followed a different pattern than what we expected. The lower reproductive output of smaller species must be related to how we defined allometrically the energetic contents of eggs. A constant percentual value for that parameter may sub estimate the reproductive strategies of smaller species. Empirically, studies showed different relationships between reproductive capacity and adult size (Kaplan & Salthe 1979; Gordon 1989; García-barros 2000), and this allometric relationships seem to vary according to taxa (Iverson *et al.* 2019). Also, a pattern of larger species investing less energy in reproduction is conspicuous, and explanations for this pattern have been proposed (Reiss 1985). A better parameterization for the allomeric relationships in our model could make it more realistic. In some empirical studies, however, the offspring numbers showed a similar relationship to what we found, with higher offspring numbers in species with intermediary sizes (Berrigan 1991). A better examination is necessary, but we can also argue that this may be a result of the energetic dynamics. The costs for maintaining maturation, for example, may be proportionally more relevant for smaller species which ingest much less energy daily, and this is a functioning that could lead to those results. We reaffirm, however, that further investigation is necessary on that subject.

We must also discuss how the DEB parameters affect body sizes and how body sizes affect population dynamics. In accord to DEB theory, as it was observed, body sizes are affected by ingestion capacity, the kappa-value and the growth energy (van der Meer 2006; Kooijman *et al.* 2008). Our model predicted that feature correctly, even as we did not incorporate all of the principles of the theory. DEB theory also predicts that resources density affects body sizes (Kooijman 2010), and that is something we could only predict indirectly in our approach. We used constant food levels on all simulations, and therefore the effect of food density cannot be formally evaluated. But we also showed differences in body sizes achieved from isolated individuals in abundance scenarios and competing individuals from population scenarios. Therefore, we confirm that prediction, assuming that competition decreases the accessibility of food by organisms, and organisms in dense populations achieve lower body sizes. The obtained relationships between the parameters and populational body sizes are probably dependent on the resource levels we simulated, and changing those levels might lead to different size distributions. Body sizes in population runs, that simulate “field” conditions, were also affected by growth energy, a parameter that doesn’t affect maximum body sizes on isolation, but interacts with life history and the system dynamics and influences body size in those “real life” scenarios. The difference between body sizes in isolation and body sizes in populations could reveal a lot about the ecological processes governing populations, and empirical approaches to that question are somehow lacking.

We made predictions on how population dynamics change according to body size, and they match what was expected by other works, such as (Savage *et al.* 2004), which predicts that carrying capacity or density at equilibrium should be negatively related to body size. It is also possible, however, that this relationship is affected by the resource quantity levels, both in its’ magnitude and shape. We consider that more exploration on those processes, changing resource scenarios, could be interesting to further understand that prediction. We also performed simulations on what should be the viable combinations of DEB parameters from a populational perspective. Again, viable combinations of DEB parameters might change on different resources conditions, because higher resource availability may help some populations of larger organisms, and evaluating this might help explain species' strategies on environments with different quality or productivity. Measuring how DEB parameters covary in different ectotherm groups and locations in reality could be an interesting validation attempt, as we would expect that those covariations would be similar to the ones that generated viable populations in our work. DEB theory is a rapid growing field, and due to new collections and empirical efforts a large-scale evaluation of those covariations may be possible (Marques *et al.* 2018; Augustine & Kooijman 2019).

The population dynamics and the population cycling we obtained can also be related to earlier theory. Cycles in population dynamics are often understood as the effect of a time delay on competition, but they may also be caused by factors like weather fluctuations, predation and parasitism (Klemola *et al.* 2010; Myers & Myers 2018; Oli 2019). Density-dependent delay is related to the generation time of organisms, when conditions that define reproductive output are not the conditions in which novel organisms actually participate in the populations (because of gestation/hatching periods in which organisms do not feed). Otherwise, it may also be caused by delays in mortality (Klemola *et al.* 2010). We see a similarity of our results to that rationale, as species with larger body sizes (and consequently longer life histories) showed greater relative population fluctuations. This allometric pattern on population oscillations, which happened even on fixed temperature scenarios, is concordant to empirical patterns and other theoretical predictions (Calder 1983; Peterson *et al.* 1983), although those assessments are often directed to endotherms, as their cyclic behaviors are not so related to climate. Other mathematical models showed that temperature change can also change the stability of systems, generating population cycles (Vasseur & McCann 2005). A curious finding of this model is that temperature change, overall, did not change the variation patterns of fixed temperatures, although there is a clear effect of reduction on mean numbers (especially in the optimum temperature).

The thermal performance curves for reproductive and growth rates follow a pattern that seems realistic, although we incorporated linear energetic efficiency responses. This is an interesting emergence, that surely needs more investigation to be better understood. We also found that the relationships between abundance and temperature regime may follow a variety of different shapes, and this is an effect of the interaction of life-history and the energetic dynamics, as all species simulated had equal temperature sensitivities. We found that higher temperatures led to larger mean body sizes overall, although it also led to lower variation in body sizes. This is contrary to empirical evidence, as the temperature-size rule is very consistent for ectotherms (Gilbert & Raworth 1996; Atkinson & Sibly 1997). There is still doubt on what are the causes for the temperature-size rule, and explanations are related to eco-physiological constraints (Berrigan & Charnov 1994; Angilletta & Dunham 2003; Walters & Hassall 2006) or to evolutionary processes (Kozłowski *et al.*

2004; Arendt 2011, 2015; Edeline *et al.* 2013; Vangansbeke *et al.* 2020). More investigation should be done to understand this emergence of the model, and could be helpful on discussing the causes of the temperature-size rule.

A very meaningful unexpected result is that of a subtle suboptimality of populations in variable scenarios. The populations showed larger abundances not exactly on optimal temperatures, but around 0 and -1 degree relative to the optimum in variable scenarios. Temperature suboptimality was already predicted by thermal ecology, but oriented to individuals, and not populations. In thermal ecology, suboptimality is proposed for thermal preference (Martin & Huey 2008; Asbury & Angilletta 2010), and predicts that organisms should prefer cooler temperatures than their optimum, either to avoid risks of overheating or because fitness benefits for adapting to high temperatures are important. The populational suboptimality we obtained could be explained by two rationales: as a consequence of temperature variation (Estay *et al.* 2011), as also proposed by thermal ecology, or because of competition (Ohlberger *et al.* 2011; Johnson *et al.* 2015). Theoretical explorations of the role of temperature variation in driving population dynamics show how variation may cause counter-intuitive effects on population growth (Estay *et al.* 2011) and different effects based on the range of temperatures which organisms experience (Estay *et al.* 2013). Models also show that the density-dependent pressure might be stronger on optimal temperatures (Johnson *et al.* 2015), and this rationale may also apply to our model. A deeper investigation is necessary, though. Further manipulations of the environmental conditions and simulating species with different sensitivities (species that could be more specialist or generalist) can generate explanations for that emergence. Those two results of the temperature effect, together, reinforce how we should be cautious when scaling individual fitness to higher organization levels. The need to understand how individual-level phenomena scale up to population levels has already been acknowledged (Kingsolver 1989), and our work reinforces the argument that mechanistic models explicitly modelling population demography can be useful for this type of advances.

Assumptions and limitations

All models may include unrealistic assumptions and our model is not an exception. Those assumptions obviously jeopardize our capacity to compare our results to the reality. But, at the same time, the model building was performed so that those assumptions could be easily modified, or the sub-models, enhanced. Therefore, those limitations also mean new opportunities for investigating different questions. The first process that shows limitations is the food production. Resources production is constant and unaffected by consumption. Although it may be realistic for some cases, it probably is not in a lot of them. The foraging sub-model is also simplistic, on how competitive abilities and feeding behaviors are modeled. Modifications and enhancements on the foraging and food production sub-models could be used to build prediction on some interesting questions. For example, theoretical investigations have revealed that differences of competition capacity between different life stages or body sizes may affect system stability, by promoting cyclic dynamics, and the characteristics of those cycles can be different depending on how juveniles or adults are superior to each other (Roos & Persson 2003). As investigations showed that some processes can only be elucidated through IBMs (Uchmánski 2000), revisiting some of those questions with this model could be interesting.

We also assume that all species have the same thermal sensitivity, and that they are uncapable of thermoregulating. This first assumption doesn't affect the dynamics per se, but exploring the patterns generated by different sensitivities could be interesting. It would be possible, for example, to use to the model to understand how species that are more generalist or specialist can display different relationships between abundance and temperature, how they can be affected by temperature variation and how their optimal energy allocation strategies could be different. We could compare those results to what has been proposed by classical optimality theory (Lynch & Gabriel 1987; Gavrilets & Scheiner 1993; Gilchrist 1995), for example. It would also be possible to compare how different trade-offs in thermal performance curves' shapes could influence macroecological patterns of abundance. Thermoregulation is an important feature that could affect the dynamics. Models of thermoregulation are usually based on the energetic expenditures of this behavior (Huey & Slatkin 1976; Vickers *et al.* 2011), and those expenditures and their consequences could be easily incorporated in the energetic dynamics of our framework. We also assume a simplistic temperature regime, in a coarse temporal scale, and enhancements in this parameterization could be also interesting. There are also some parameters in which we used assumed values or allometric relationships. Some of those parameters clearly affect the system, and a more careful parameterization would be productive. A very important assumption is the lack of intra-specific individual variation, but that is a feature we will explore in the next chapter of this thesis.

Conclusion

In our evaluation, the modelling approach we developed here was productive, and has the potential to be interesting in further assessments of ecological systems. We generated a model with a relatively high level of detail that fulfilled the role of a paradigmatic exploration of population dynamics by a generalist approach. The IBM we developed simulated well some of the most important drivers of population dynamics, on a macroecological perspective, but also generated some controversial findings that can be relevant for ecological theory. The idea of using DEB theory to generate random species was interesting, as it allowed us to generate complex dynamics with the usage of a small number of parameters. In this framework body size emerged from the interaction of the energetic parameters, and population dynamics emerged from energy usage and its' relationship with the environment. We evaluate that DEB theory really stands as a useful theoretical body for standardization of sub-models on IBMs, and reinforce that the scaling up of individual fitness to higher organization levels might be very complex. Our model is bound to some assumptions that are not realistic, but we discussed how enhancements on those limitations can be interesting for more investigations, which we wish to address in future work.

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CHAPTER 3 – CONSEQUENCES OF INTRA-SPECIFIC THERMAL TRAITS VARIATION AND HERITABILITY FOR MICRO-EVOLUTIONARY PROCESSES AND POPULATION DYNAMICS

Abstract

The need to understand how species would react to climate change presses ecologist and evolutionists to assess what are the real possibilities for populations to adapt to environmental change. Several theoretical assessments to this question have been performed, by genetic quantitative models, range dynamics models and evolutionary rescue approaches. In this work, we try to advance on this perspective by using an individual-based model accounting for more detailed population dynamics and explicit relationships between organisms' intra-specific variability and the environment. In this work, we used the population model developed in the second chapter of this thesis to generate random species for analysis and incorporated intra-specific variability and heritability to the thermal traits, to understand how adaptation would happen through emergent fitness changes. Our results are highly concordant to earlier theory, suggesting that this model reliably simulates the system and can be interesting for further investigation on adaptation processes. Incorporating other forms of variability (for example on energetic parameters), more complex sub-models (for greater realism on thermal responses and behavior, for example) and a spatial structure are probably the most interesting enhancements for further usage of this approach.

Keywords: individual-based model, adaptation, evolutionary rescue, population dynamics, demography, mechanistic model.

Introduction

The capacity of populations to adapt to novel or local environments is a crucial question on ecological research, either to understand the dynamics or drivers of species ranges or to understand impacts of environmental change (Burger & Lynch 1995; Chown et al. 2010; Elith *et al.* 2010; Phillips 2012; Bay *et al.* 2017). Temperature is probably the most important among environmental factors, as it affects organisms' physiology (Clarke 1991; Somero 1995; Somero *et al.* 1996; Fields 2001) and consequently higher organization levels as population dynamics (Walker *et al.* 2015; Mccardle & Fontenot 2016; Cherkiss *et al.* 2020) and evolutionary processes (Rohde 2013; Gillman & Wright 2014). The relevance of local adaptation to temperature regimes is recognized, as empirical efforts has shown variability in thermal traits of various species (Hughes *et al.* 2009; Bruijning *et al.* 2018; Miller *et al.* 2020), thermal adaptation via experiments (R.B. *et al.* 1991; Bennett *et al.* 1992; Padfield *et al.* 2016; Pereira *et al.* 2017; Chen *et al.* 2018) or performance clines (Magiafoglou *et al.* 2002) and genetic basis for variability and adaptation of thermal traits (Munday *et al.* 2017; Chen *et al.* 2018; Miller *et al.* 2020). Although all those evidences suggest local adaptation is sure to happen in large time scales, there is still mixed evidence on the capacity of the species to adapt to thermal regimes throughout small numbers of generations, as some studies show it is possible for some species (Padfield *et al.* 2016; Bodensteiner *et al.* 2021) while others do not (Hinder *et al.* 2014; Wooliver *et al.* 2020).

Mathematical models helped theorizing on which conditions fast thermal local adaptation is expected. Their general lessons are 1) populations follow the environmental change with a time lag (Burger & Lynch 1995; Kuparinen *et al.* 2010), that is affected by the advantages of adaptation on fitness and initial genetic conditions (Burger & Lynch 1995; Chevin *et al.* 2010; Bay *et al.* 2017), 2) the capacity to follow change depends on other factors related to demography (Gomulkiewicz & Houle 2009; Schiffers *et al.* 2013) and the steepness of environmental change (Pease *et al.* 1989; Burger & Lynch 1995). Those models usually were based on differential equations or state-variable approaches, but recently individual-based models were also used (Schiffers *et al.* 2013; Dytham *et al.* 2014). The most basic and general models are usually based on a population whose fitness is defined by a heritable additive trait. Those populations are exposed to a gradual environmental change in an axis, and the capacity of the populations to "follow" that axis is evaluated under scenarios of selection (Pease *et al.* 1989; Burger & Lynch 1995; Bürger & Ghnelfarb 1999; Gomulkiewicz & Houle 2009). The theoretical explorations got more complex, as models tend to incorporate more sophisticated features like explicit demography (Coulson *et al.* 2010; Schiffers *et al.* 2013; Dytham *et al.* 2014) and temporal/spatial scales to their framework (Bridle *et al.* 2010). Enhancements on modelling approaches came from rationales on the drivers of adaptation and the rise of usage of more complex models. It became obvious, for example, that accounting explicitly for population dynamics or demography was necessary (Hanski & Saccheri 2006; Kuparinen *et al.* 2010;

Lavergne *et al.* 2010; Bay *et al.* 2017), as genetic frequencies are dependent on population numbers and those population numbers might be also affected by adaptation. As empirical evidence demonstrated, responses to thermal regimes may be highly polygenic, but still most models evaluated single additive traits on their frameworks (Bay *et al.* 2017). Some assumptions of those models were criticized, as for example the need to assume fitness functions, which are often unrealistically constant in time (Delong & Gibert 2016). Individual-based models are a more complex approach that can be ideal for exploring those critiques. They have been applied to this question, but often not really addressing the limitations. Even those still needed to assume fitness functions for the relationships between traits and the environments (Gomulkiewicz & Houle 2009; Phillips 2012), and population dynamics or demography was often incorporated on simplistic manners, for example not incorporating life cycles explicitly (Schiffers *et al.* 2013; Dytham *et al.* 2014). Models which were able to surpass those assumptions were prone to loss of generality, as they were built and parameterized for single species (Piou & Prévost 2012).

We consider that an approach exploring the functionalities of individual-based models would be useful for studying fast local adaptation, especially to temperature. Individual-based models are ideal for exploring detailed life cycles and individual interactions (Judson 1994; Grimm 1999). In the second chapter of this thesis, we developed a population model whose dynamics emerge from the organisms' responses to temperature and their resources usage through energy budgets. We showed a detailed approach for population ecology that could, still, be general. We believe that exploring local adaptation, as it emerges from mechanistic interactions between the species and the environment in a general approach is an interesting way to study local adaptation.

In this contribution, my objective is to develop the model presented earlier (see chapter 2), incorporating intra-specific variation and heritability in thermal traits to the framework, so that it is possible to build predictions on the species' capacity to adapt to different thermal regimes in small time scales. It is important to build this model using the structure presented in chapter 1, as this will allow us to understand those capabilities explicitly accounting for demographic impacts of warming and adaptation. In the biological realm, the adaptation of the species if affected by demographic factors as well as the environmental pressures, but the demographic patterns are affected by environmental pressures as well. Modelling approaches on this question, to date, have frequently incorporated demographics in a simplistic and implicit manner, and that is a limitation that we wish to explore in this study. I wish to answer the questions 1) how thermal regimes and species characteristics affect their capacity to local adaptation, 2) how this adaptation can mitigate the effect of stresses in the population level and 3) how the predictions built in this study relate to what is already predicted for those questions. We believe that advancing on those directions might be useful for further theoretical understanding.

Methods

OVERVIEW

In this chapter, we advance from the model developed in chapter 2, incorporating variability and heritability in the thermal traits of the organisms. To avoid unnecessary repetitions, we provide a brief review of the models' concepts, as the model is explained with detail in the last chapter. In that model, species are ectotherms defined by their energetic expenditure processes and temperature sensibility. Organisms compete for an amount of food that is daily produced by the environment, and allocate the energy obtained for somatic or reproductive processes. The organism' life stage (egg, juvenile or adult) dictates details on how that energy is allocated. Environmental temperature dictates the efficiency of energy usage/capturing for 3 physiological processes: food assimilation, somatic maintenance and individual growth. As chapter 2 showed, some important processes on the model are emergent: 1) Organisms' body size and reproductive capabilities emerge from the species energetic parameters, and therefore individual fitness and populations growth are also not calculated or assumed, but emergencies; 2) density-dependent regulation, that emerges from how organisms randomly acquired resources produced each day; 3) thermal performance curves for whole life processes and population dynamics emerge from how details of energetic expenditures interact with harsh temperatures.

The model is based on two theoretical fields which are overall very known and tested, which are DEB theory (van der Meer 2006) and thermal ecology (which we reviewed in the first chapter of this thesis). The models' objective was to use those theories to generate random species and perform an analysis of what they would predict for population dynamics, serving as individual-based "standard model" for population dynamics. We believe that developing from this model is ideal for the question of this chapter, because 1) it explicitly considers demographic processes, and does that in a mechanistic fashion, based on the highly validated DEB theory, 2) it is an Individual-based model, and therefore is ideal for incorporating individual variation and interactions, and 3) it also incorporates the effect of temperature in a mechanistic manner, based on some principles from thermal ecology. We believe that parting from that model will be ideal to overcome some already discussed limitations in the modelling of thermal adaptation, like explicitly incorporating demography and treating fitness as an emergent factor, and not an assumed function.

In order to model adaptation to thermal regimes in a mechanistic fashion, we must incorporate intra-specific variation in thermal traits, and also make this variation heritable. We used the same algorithm of the previous model, adding the following features: 1) in addition to the previous attributes of the individuals, they also possess a vector containing paternal and maternal genes (1 or -1 genes, which represent genes more adapted to hot or cold regimes, respectively), which change their sensitivity to temperature and 2) a complementation to the reproduction submodel, in which females now reproduce coupled to a random adult male and their eggs receive random genes from the two parental organisms. Those incorporations added two new parameters to the model: one is *f*, that is the effect that each gene causes on the organism' thermal response and *n*, that is the number of loci that influence each life processes, and is related to genetic diversity of that process. With those enhancements, individuals should respond differently to temperature, and according to those effects, better adapted individuals should produce more offspring and then adaption should occur through a change of allelic proportions in the population. The individuals advantage coming this difference of performance will be an emergent feature, and the manner that this translates to populations and genetic frequencies will also emerge from the whole system. We will simulate an emergent occurrence of evolution by the basic premises of natural selection: a variation in the organisms, that is related to fitness and heritable. It is important to note that the model will function through random crossing and explicit population numbers, so genetic drift is also emerging from the system.

SUBMODELS

Intra-specific variation in thermal responses

We assume that individuals have some genetic loci that change their thermal performance curves (figure 1). Three functions are affected by temperature: food assimilation, somatic maintenance and growth, and each of those functions will have different locus affecting their performances. This means that, differently from the model of the chapter 2, organisms now may display different performance curves for each of those 3 processes. Those loci may generate proteins which are adapted to high temperatures (1 values, shifting the optimum of the response towards hotter temperatures) or low temperatures (-1 values, shifting the optimum of the response towards colder temperatures). The amount of the shift caused in the performance curves for each gene is dictated by the parameter f, that is measured in Celsius degrees. For our analysis, we will assume that this parameter has the value of 1 degree. For each locus, two genes will be present, a paternal and a maternal one. We assume no linkage structure in the heritability of those genes, and also no dominance in their expression. We assume a simple pattern of evolution of TPCs: they change their location in the temperature axis, therefore their optimum, but do not change their shapes.

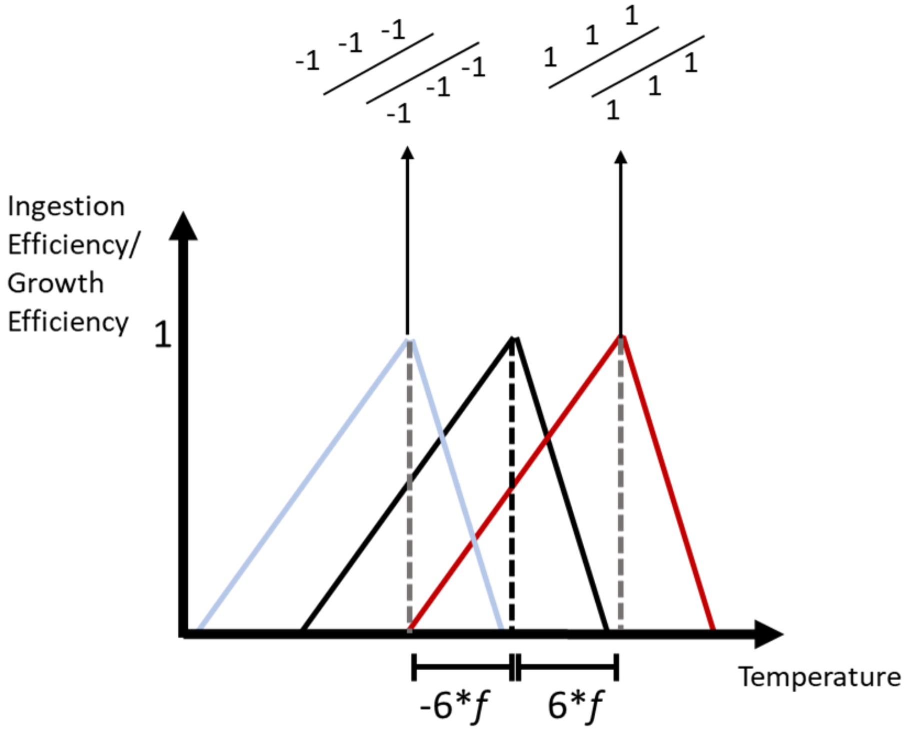

Figure 1: A representation of how intra-specific variability occurs in the model. The genes change the optimum of the organism, by an amount of f degrees Celsius. An individual with only -1 genes is a totally cold adapted organism, and an organism with only +1 genes is a totally warm adapted organism. Each organism now can have 3 different performance curves, one for each energetic process.

Random reproduction and heritability

Reproduction follows the same processes as in the second chapter. The additions are: 1) females reproduce coupled with a randomly selected adult male, and 2) offspring now inherit the genes from their generators (figure 2). We assume that there is no difference in sexual competition from different individuals, and therefore the coupling is completely random. At each oviposition cycle, a female is coupled to a random male. For simplicity, each female can be coupled to only one male, but males may couple to more than one female or none. Regarding the offspring, each egg, for each locus, receives a random paternal and maternal gene from their progenitors, according to that locus (figure 2). Overall, reproduction is defined by random crossing of males and females and random heritage for each of the loci. For simplicity, we assume that those loci have no structural linkages and no dominance. We also assume no possibility for mutation or ingression of new genes by migration. We do not need to assume a specific form for selective pressure (stabilizing or directional) as it will be an emergent feature.

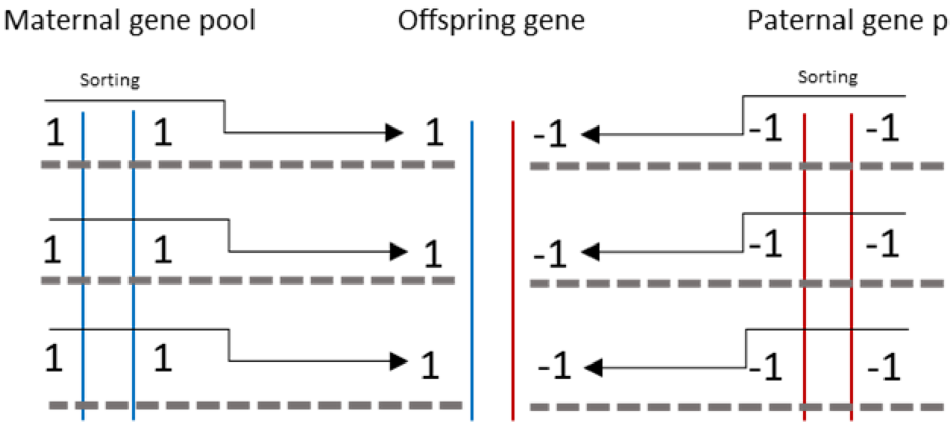

Figure 2: A representation of how heritability happens in the model. Offspring receive a random gene from their paternal and maternal pools, according to each locus.

Observation and Analysis

We ran populations on different scenarios (figure 3) for 100 years. Those populations were of 71 randomly generated species, that are the species that did not go extinct on neutral temperature scenarios from the analysis of chapter 2. Those populations started with 20 individuals each, and those individuals had an equal ratio of '1' and '-1' genes in their gene pools. The scenarios were run for: 2 different temperature variation regimes, a fixed scenario (-8, -4, 0, +2, +6 degrees celsius) and fluctuating scenarios of +-3 degrees of variation (figure 3a), 5 different temperature change regimes figure 3a), and 3 levels of genetic diversity (1, 2 and 3 loci for each physiological function, resulting in 3, 6 and 9 loci in total, respectively, as figure 3b). We chose an asymmetrical range of temperatures for the simulations, because the model we used assumes asymmetrical relationships of the temperature effect (the effect of cold environments is more amenable), and by this we capture interesting and more relatable temperature ranges from hotter and colder regimes. We assume that *f* is always 1.

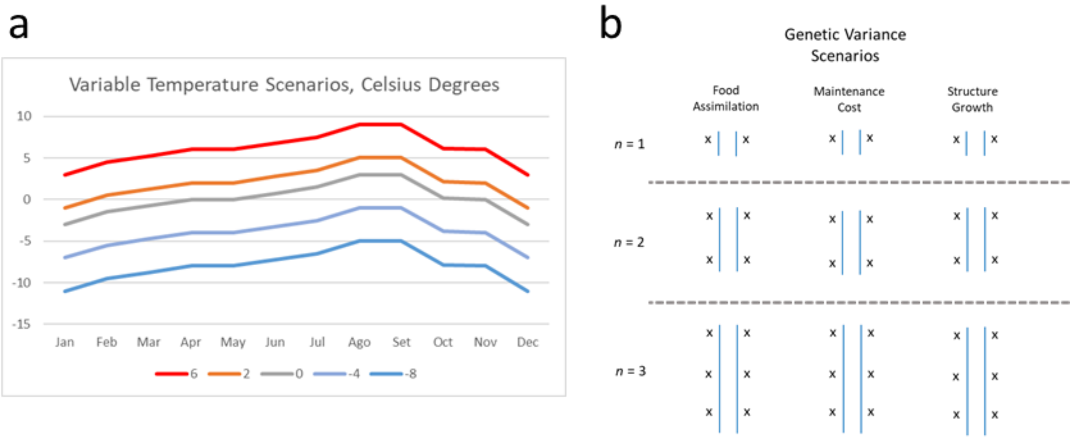

Figure 3: a representation of the fluctuating temperature scenarios (a) and the genetic diversity scenarios (b). The temperature scenarios are monthly means in 5 change scenarios with a variability of +-3 degrees. The genetic variance scenarios are the number of loci affecting each energetic process (n).

For each run of the model, we recorded at each of the 100 simulated years 1) the mean of abundance and standard deviation of abundance for that year and 2) genetic proportion in the population (relative quantity of -1/+1 genes) in the last day of that year, leading to 3 vectors of 100 values which slope represents the rate of change on those statistics in the system. For each of those runs, we also recorded the final genetic proportion on that population, representing how they adapted to hotter or colder environments at the end of the simulation. In this model, genes are qualitatively defined as -1 (cold resistant gene) or +1 (hot resistant gene). The usage of those exact values helps in model analysis, as the sum of all genes of a population or an individual also shows the frequency of those genes in that population or individual. For example: in a scenario of n=2, an individual has the sum of the genes for a trait variating from -4 to +4, representing an individual totally adapted to cold and hot environments, respectively. In that same scenario, in a population, means of all genes also lead to a range of -4 to +4, and in those cases the extremes also represent a population fully adapted to cold or hot environments, at the point in which genetic variance is lost. By using those sums, we can easily account for frequency and phenotypic change in the same value.

We used multiple regressions to understand how species characteristics (the maximum species' body size) and the scenarios (temperature variation, temperature change and genetic diversity) explain the demographic and genetic dynamics of the system. We performed further analyses on which factors could explain populations that got extinct, using logistic regressions. Using statistical tests for modelling results has some conceptual problems, but we intend on using those models as exploratory tools and not as standard hypothesis testing.

Results

We present an example of a model run in figure 4. A random species from the pool which we simulated, of maximum body size 83 cm^3, is shown in scenarios of '+3' and '-4' degree changes for fixed and variating regimes. We show how genetic proportions and population dynamics happened through 100 years of simulation. This example run shows a species with a very fast adaptation capacity, that adapted for hot or cold environments in approximately 20 years. We can see that there are environmental change "steps" in which gene fixation is possible (proportion reaches -2 and 2 values). In temperatures in between those genes, however, genetic diversity is maintained (the fluctuating lines of 3 loci scenarios).

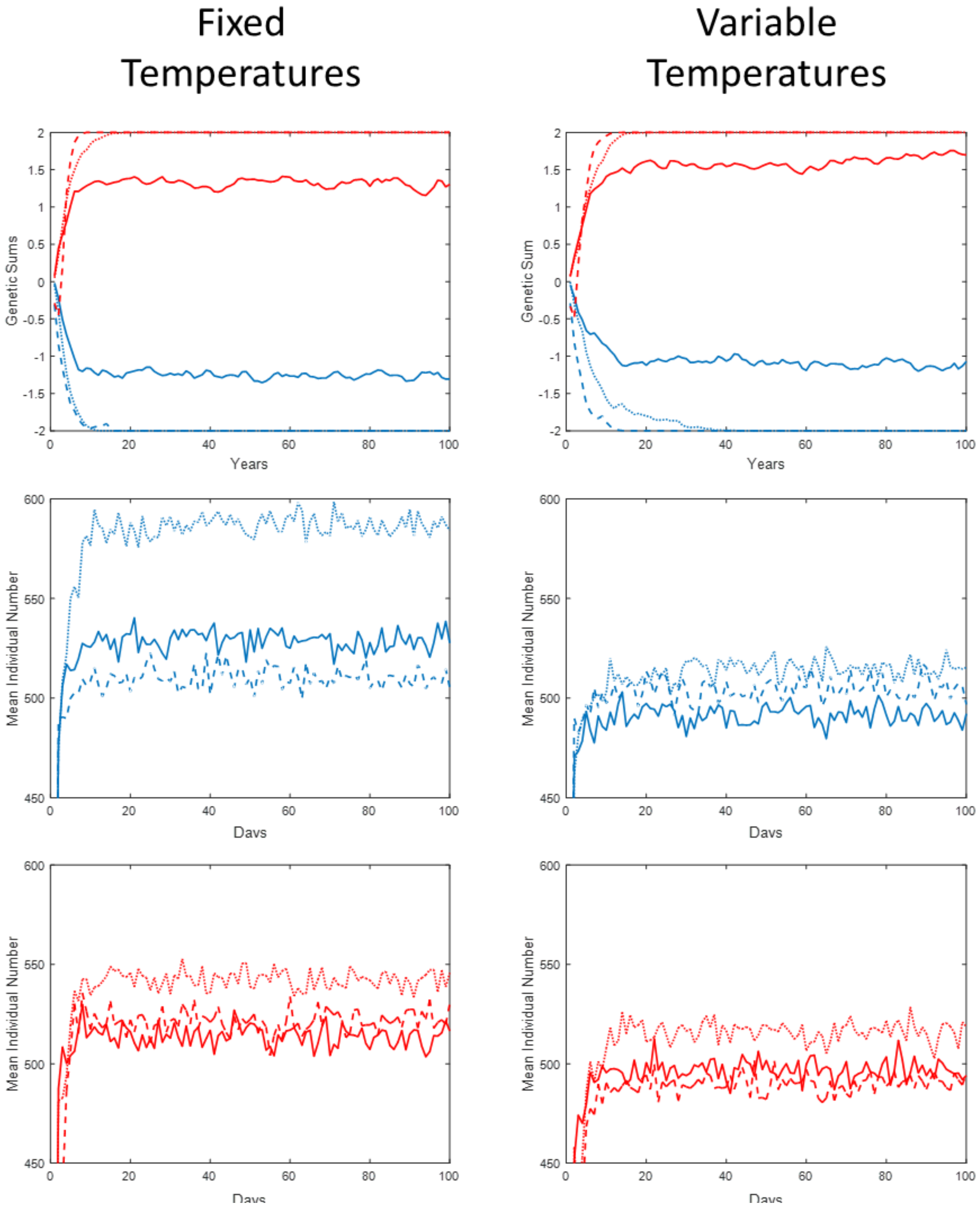

Figure 4: runs on a single species for exemplification of model dynamics. The species has a maximum body size of 83 cm³, as result of the following energetic parameters: Ingestion capacity of 113 energy/body surface, kappa-value of 0.6, maintenance energy of 15 energy/body volume, and growth energy of 772 energy/volume. A species is run in fixed (left) and fluctuating (right) temperature scenarios, for +3 (red line) and -4 (blue line) degrees relative to optimum, and 1 (dashed line), 2 (point line) and 3 (continuous line) locus quantities. Upper graphs show frequency through the sums of genes, ranging to a total of +2 (all genes in the population are +1) to -2 (all genes in the population are -1). Bottom graphs, separated by temperature regime for clarity, show population dynamics.

At first, we notice that there is an effect of the new additions on population dynamics (table 1). The way that abundance means changed throughout the 100 years is dependent on the species' body size, especially in variating scenarios, but also by temperature change. We found an overall increase in abundance in more extreme temperature scenarios (figure 5). Figure 5 does not show very well the distributions of the effect, so we plotted them by temperature change treatment (figure 6), where it is possible to see a very different pattern especially for +6 scenarios. Declines in abundance also occurred, and apparently also on scenarios in which populations adapted. We plotted the slope of mean and variation of abundance against the slope of genetic frequencies (figure 10), and there seems to be a relationship between how fast a population evolves and the changes in dynamics. The changes in dynamics, however, display both positive and negative values, showing that species that adapted to new regimes also displayed populational declines. The changes in population fluctuation were also dependent on temperature change, but in fluctuating scenarios body size also had an important effect. In fluctuating temperatures, body size caused the decline in species fluctuations to be stronger, meaning that bigger species got more stable and smaller species increased variation (figure 7).

Table 1: multiple regression results. 4 model results (abundance mean slope, abundance deviation slope, final genetic proportion and slope of annual gene proportion) are explained by the temperature change scenario, the n parameter and the species' body size. We performed different analysis for fixed and fluctuating scenarios. Analyses were run for a total of 2.130 samples, but there are less degrees of freedom for some metrics due to extinctions.

Abundance Mean slope				
	Fixed Temperatures		Fluctuating Temperatures	
	Estimate	p-value	Estimate	p-value
Intercept	0.056	<0.01	0.059	<0.05
Temperature Change	0.0044	<0.01	0.0004	0.059
Number of loci	0.011	0.19	-0.0044	0.71
Species' Body Size	-0.000013	<0.05	-0.00053	<0.001

Abundance Deviation Slope				
	Fixed Temperatures		Fluctuating Temperatures	
	Estimate	p-value	Estimate	p-value
Intercept	0.033	<0.01	0.04	<0.01
Temperature Change	0.0027	<0.01	0.0024	<0.05
Number of loci	0.005	0.35	-0.0022	0.71
Species' Body Size	-0.000003	0.43	-3.052	<0.001

Phenotypic Alteration

	Fixed Temperatures		Fluctuating Temperatures	
	Estimate	p-value	Estimate	p-value
Intercept	-0.239	0.4	-0.11	0.7
Temperature Change	-0.37	<0.001	0.55	<0.001
Number of loci	-0.46	<0.001	0.45	<0.01
Species' Body Size	-0.00001	0.8	0.00002	0.19

Slope of Phenotypic Alteration

	Fixed Temperatures		Fluctuating Temperatures	
	Estimate	p-value	Estimate	p-value
Intercept	-0.003	<0.05	-0.0006	0.7
Temperature Change	-0.00002	0.84	-0.0002	0.2
Number of loci	-0.007	<0.001	0.006	<0.001
Species' Body Size	-0.00005	<0.001	-0.000009	<0.001

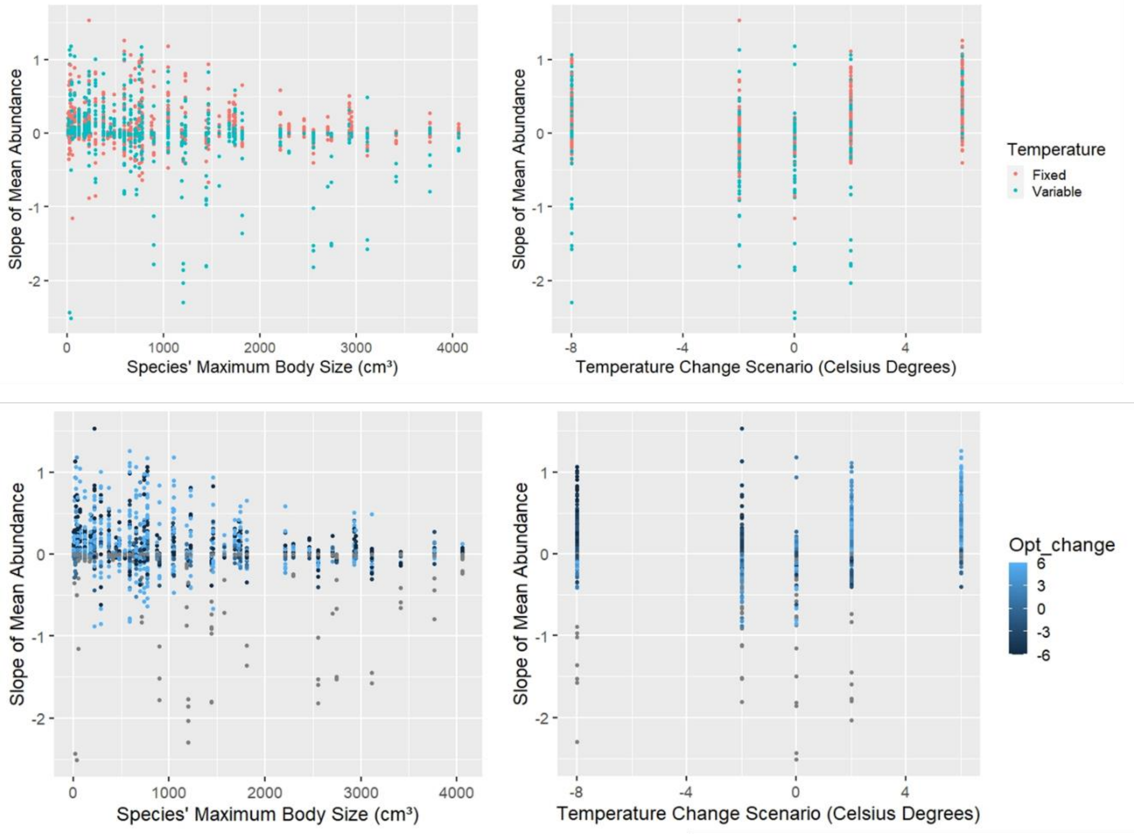

Figure 5: factors that explain changes in abundance over 100 years. Slope of mean abundance means the inclination of annual mean abundance through the 100 years of simulation. Top and bottom left show that smaller and intermediate species show higher variation in possibilities of demographic changes. Right

graphs show that the slope of abundance is correlated to the temperature scenarios and slopes of optimum change.

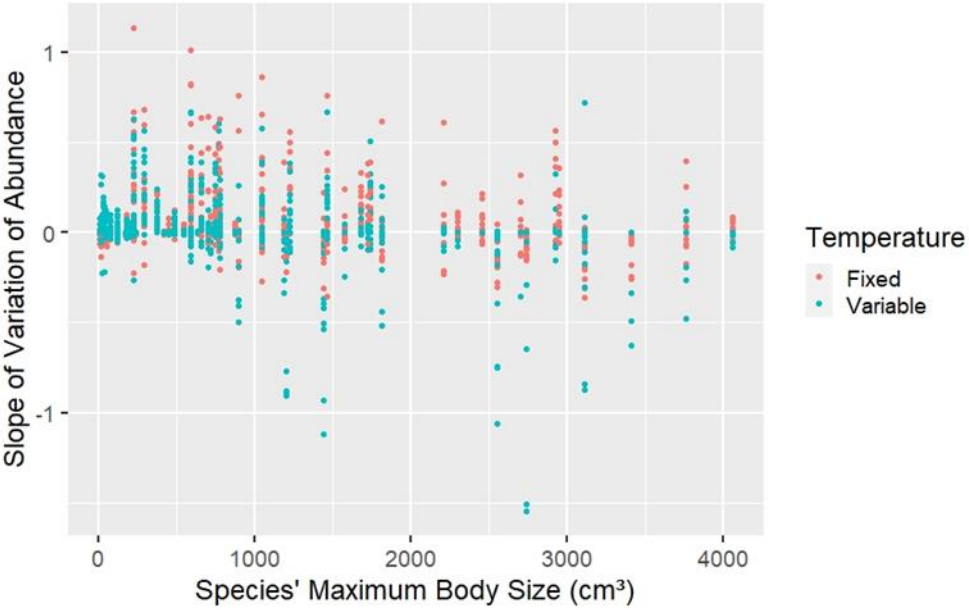

Figure 6: Patterns of how changes on fluctuation occur through 100 years of model runs show similar patterns to what happen to abundance.

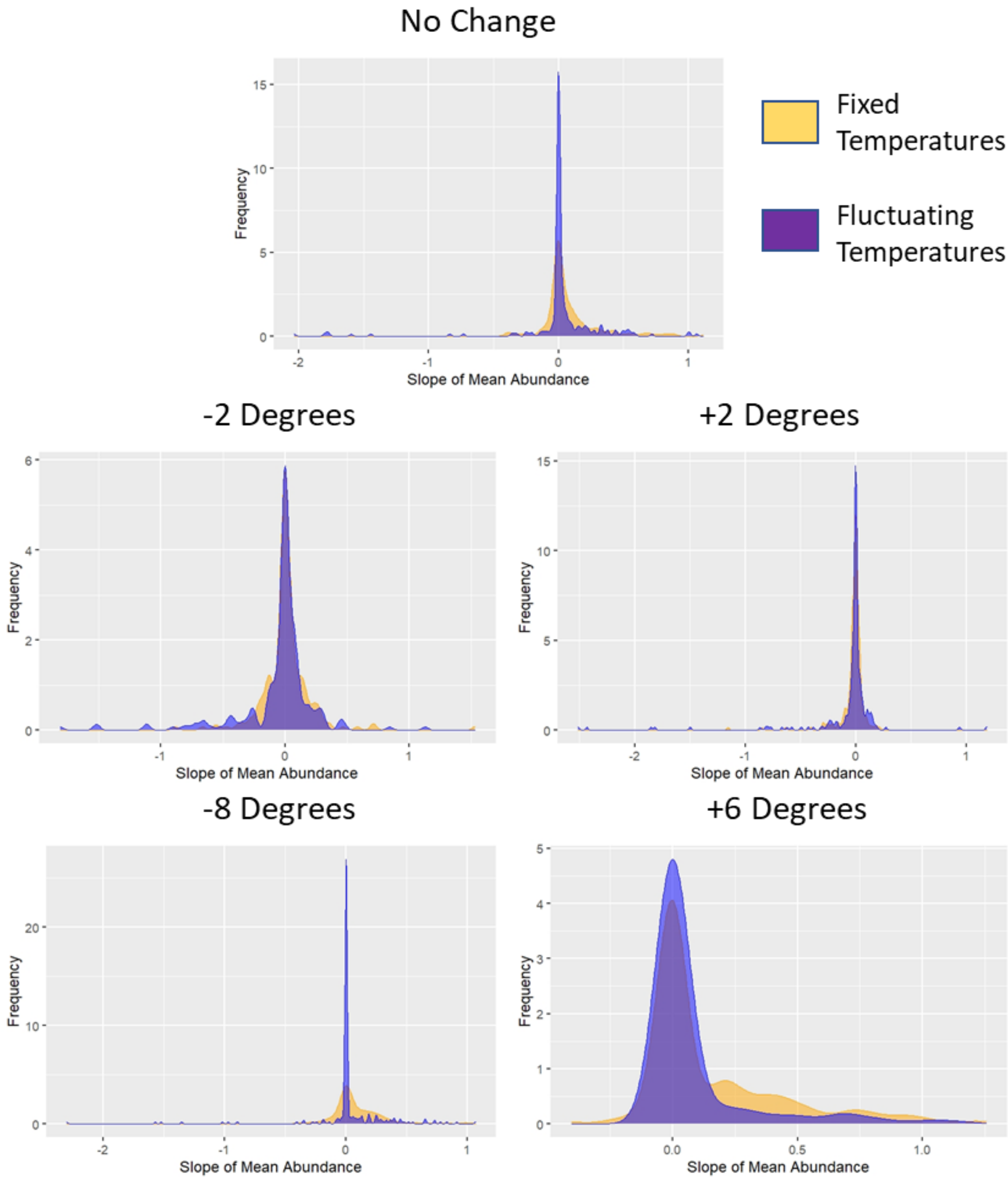

Figure 7: distributions of the slope of mean abundance (rate of change on annual means of abundance) for temperature change scenarios.

The final genetic proportion, which shows if a population adapted to a temperature regime, was affected both by temperature change scenario and by the *n* parameter (figures 8 and 9). As it would be predicted, hotter scenarios led to higher sums of +1 genes, and colder scenarios led to higher sums of -1 genes. We must notice that in the “+6” temperature scenario, adaptation was possible almost only on fixed temperatures, as in fluctuating scenarios almost all populations went extinct. We must also notice that a lot of populations did not fix their genes, especially in more mild temperature scenarios, showing also the effect of genetic drift in the system. Curiously, there were a significant number of cases in which maladaptive proportions were obtained. Some species even fixated +1 genes in -6 temperature scenarios, for example.

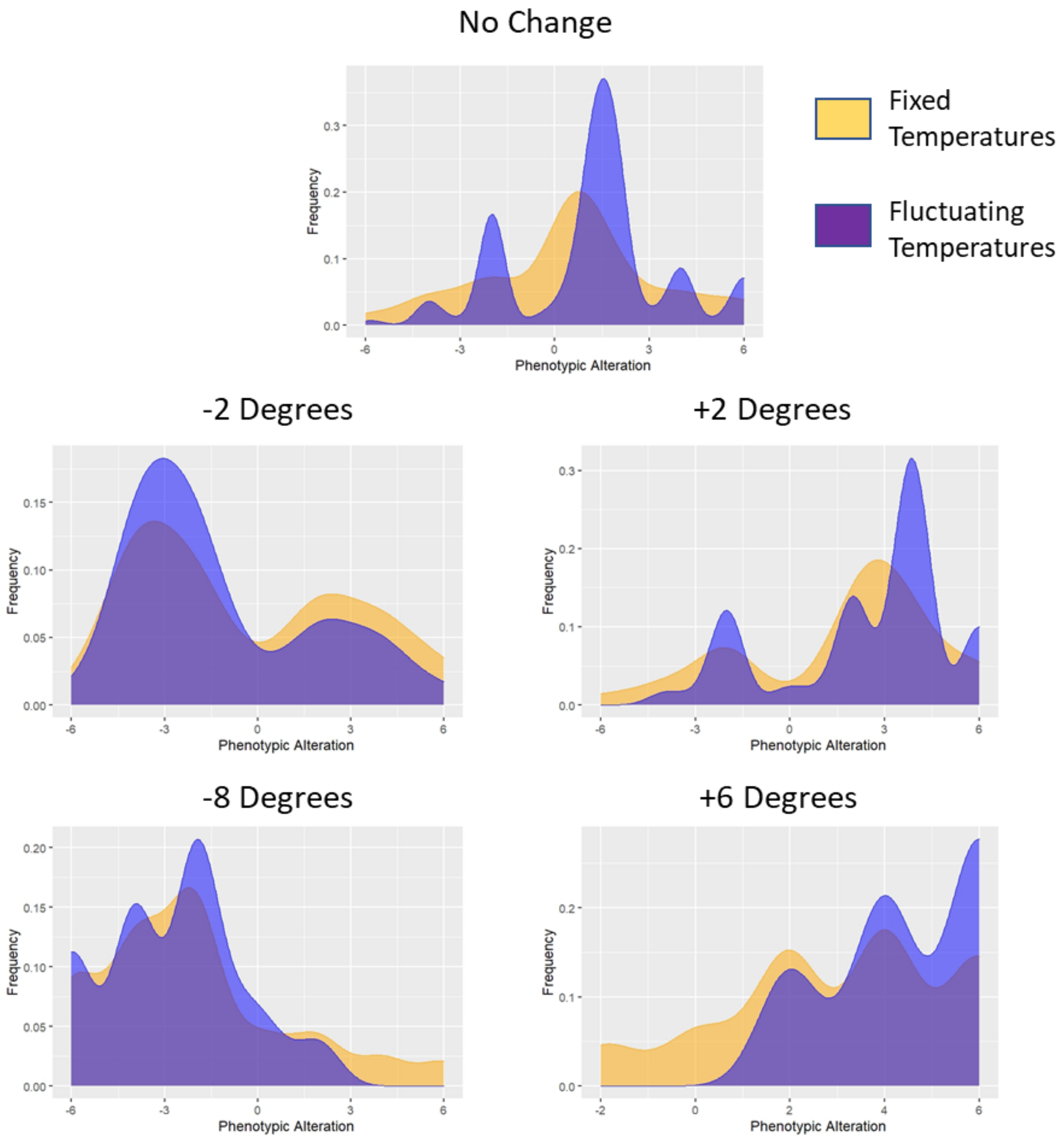

Figure 8: distributions of the final genetic proportion (genetic sums on the last year) for temperature change scenarios.

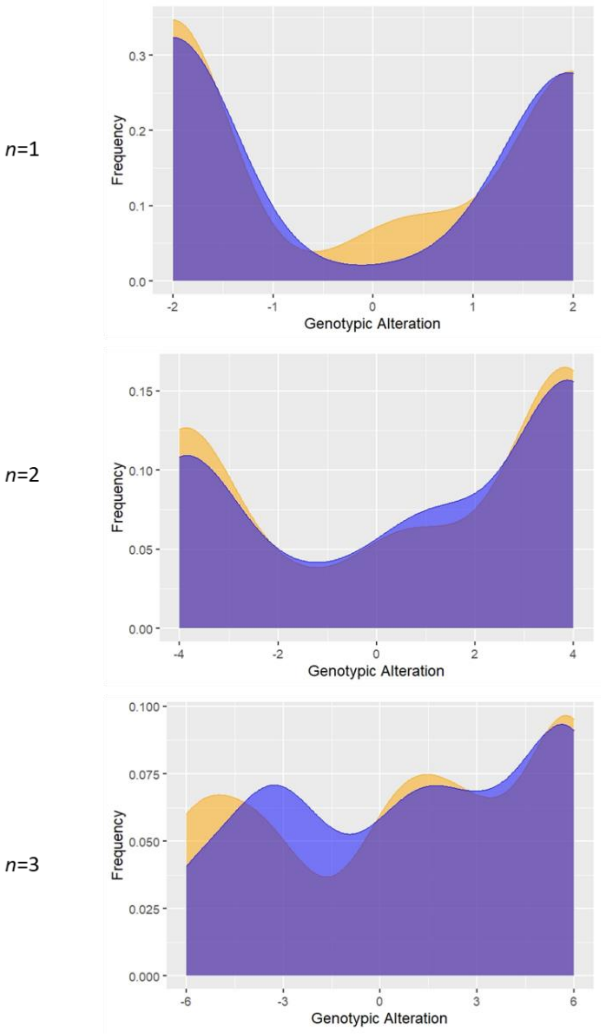

Figure 9: The genotypic change in the species was dictates by the number of loci. Distributions of the final genetic proportion are shown for each treatment of number of loci (the *n* parameters).

The slope of annual change in optimum, which represents how fast a population evolved, was influenced by body size and genetic variance, and although not shown in statistic results, it was also affected by temperature change. Temperature caused a nonlinear pattern on optimum change speed. Less extreme temperatures displayed higher values of this slope. This result probably was not clarified by the regression, because of its' nonlinear shape. The interaction between speed of optimum change, slope of abundance and body size are also clear (figures 10 and 11).

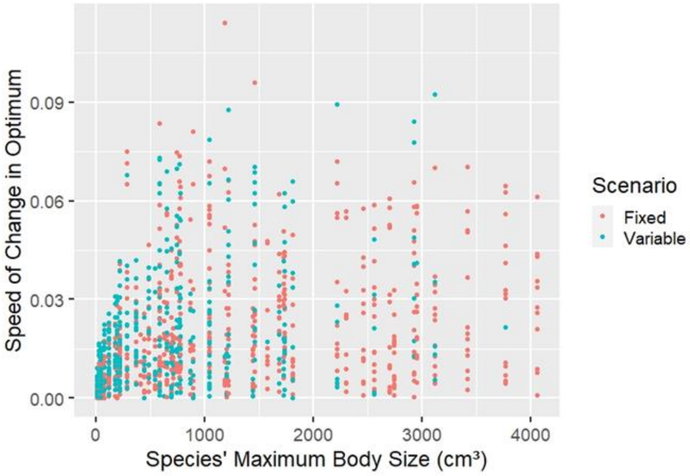

Figure 10: The velocity in which species adapted, displayed by the slope of the genetic sums through the 100 years, is faster on species with intermediary body sizes (left) and on less extreme temperature scenarios (right). Those graphs also show differences between fixed and fluctuating temperature scenarios. Temperature variation was more important in shaping the dynamics for larger species (left).

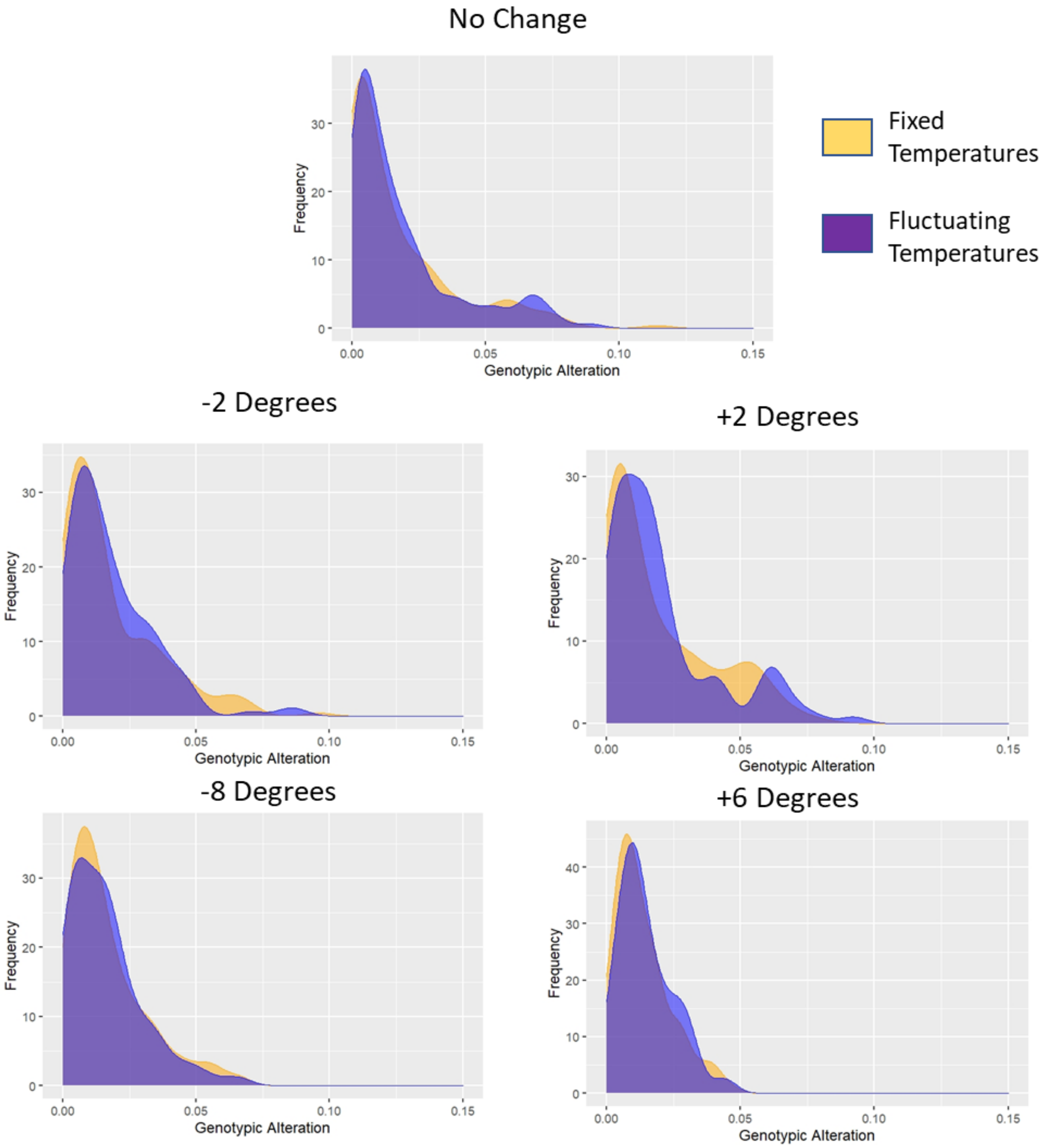

Figure 11: Distributions of the speed of genetic changes on different temperature changes and treatments.

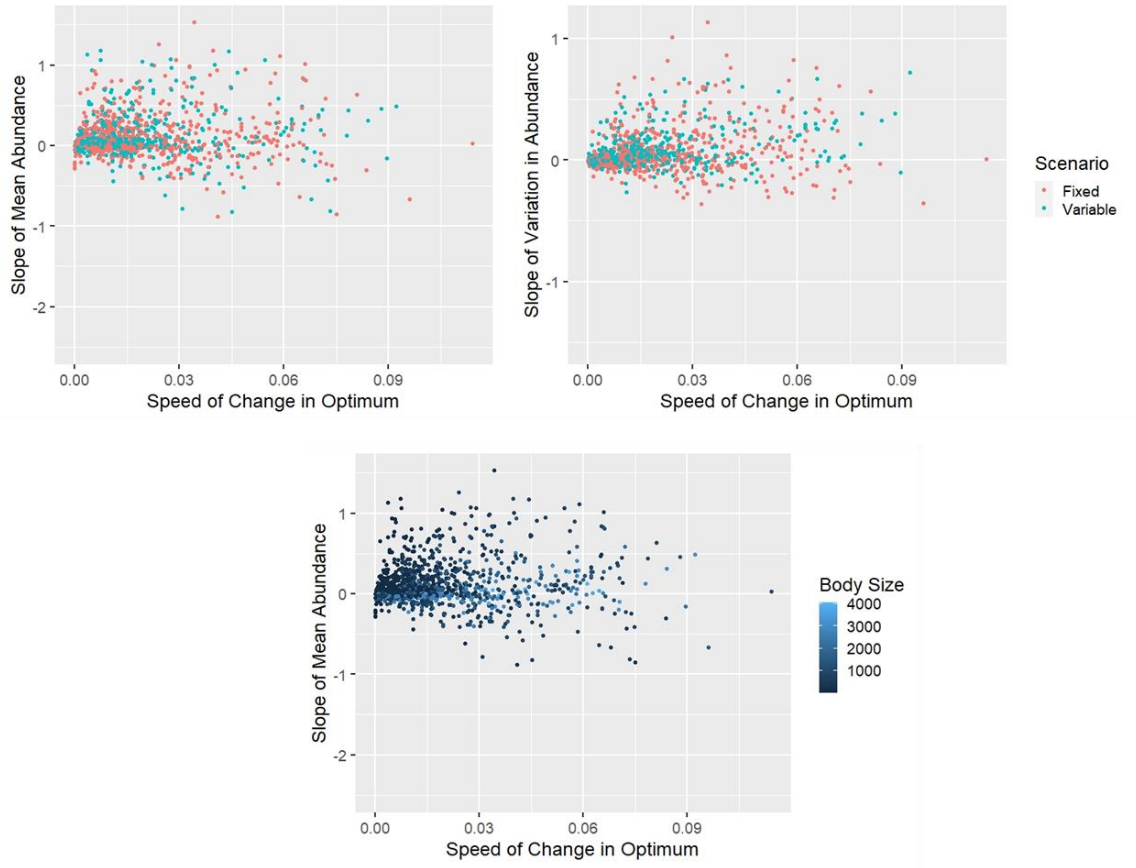

Figure 12: correlations between the slope of the yearly mean abundances and the slope of yearly genotypic sums. Fast changes in gene frequencies led to higher gains on abundance and also to losses in abundance. Bottom graph shows larger abundance gains were achieved by smaller species.

Our analyses regarding extinction are presented on figures 12 and 13. Temperature fluctuation overall increased the probability of extinctions, and changed the pattern on how body size influences the extinction probability. In fixed scenarios, smaller species were more susceptible to extinction. In Fluctuating scenarios, larger species were also susceptible to extinction. In both treatments, the magnitude of temperature change alleviated the pattern, by causing extinction in more species in a wider variety of body sizes (figure 13).

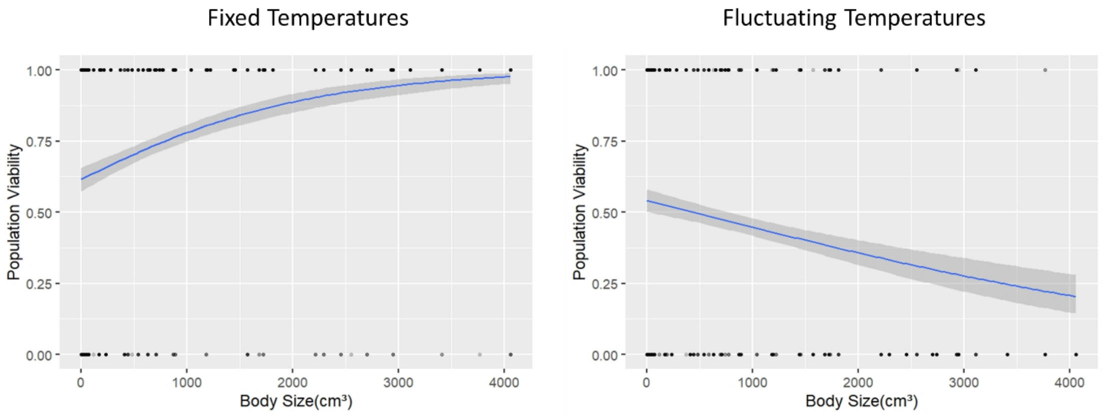

Figure 13: Contrasting patterns of the relationship between viability (viable species are those with positive population numbers after the 100 simulated years) and body size for fixed and fluctuating scenarios.

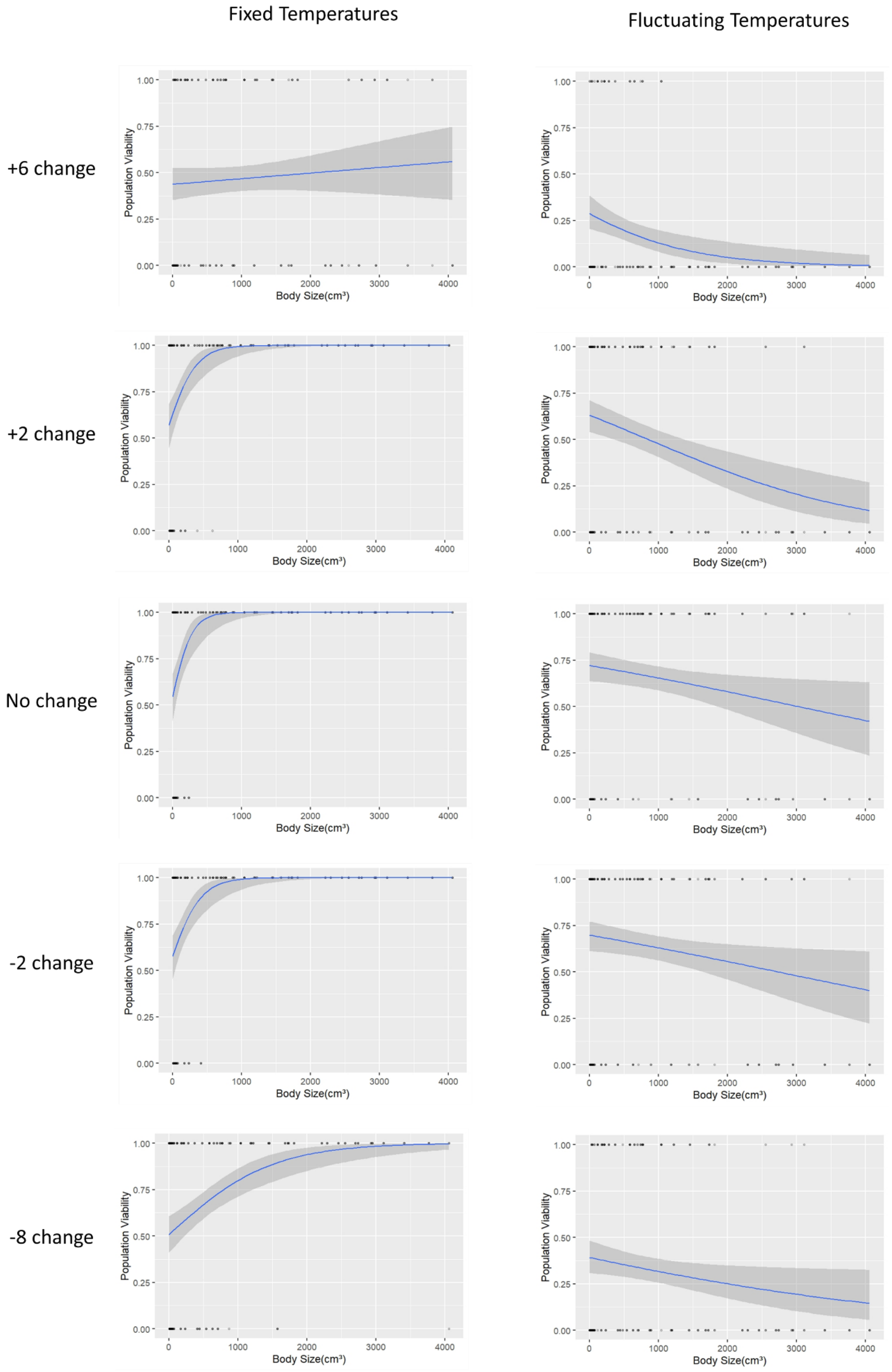
Fixed Temperatures
Fluctuating Temperatures
+6 change
+2 change
No change
-2 change
-8 change
Population Viability
0.00
0.25
0.50
0.75
1.00
Body Size(cm³)
0
1000
2000
3000
4000

Figure 14: The intensity of the relationship between extinction and body size changes according to magnitude of environmental change, especially on fixed scenarios. Plots display the fit for a logistic regression.

Discussion

In this work, we developed a mechanistic individual-based model with explicit genetic architectures to predict adaptation to novel environmental regimes. The model uses energetic budgets and environmental resources as a sub-model for populations' self-regulation, and environmental temperature affects the efficiency of the energies spent in those budgets. By this method, we generated a model in which individual fitness is an emergent feature, and the scaling between individual fitness and population dynamics is also emergent. When intra-specific variability in thermal traits were included, the relative fitness of individuals also emerged from the system, and it was possible to observe gradual phenotypic evolution and its' consequences to population numbers. It was already suggested that assumptions regarding fitness functions might be a limitation to models of adaptation (Delong & Gibert 2016), so we believe that predicting fitness on a mechanistic fashion instead of assuming it can be very interesting to some questions on ecology. Our results reinforce the view that linear or simplistic relationships between individual fitness and population fitness can be misleading, just as linear relationships between adaptation to a gradient and population numbers. In genetic models that address genetic adaptation and evolutionary rescue, heritability is often performed via sampling from a phenotypic distribution of the parental organisms (Dunlop *et al.* 2009; Carlson *et al.* 2014). In our model, we explicitly accounted for the genes. Our approach can help to simulate scenarios in which response is highly polygenic, and simulating genetic variance in more realistic ways may help understanding the effect of genetic variance in the dynamics (Delong & Gibert 2016; Bay et al. 2017).

We performed an initial exploration of the models' dynamics, in simplistic scenarios and parameterizations, to understand how the results compare to other models. This analysis showed, on a macro ecological approach, that species with different body sizes and generation times can show very different responses to environmental changes, even if their sensitivity to temperature and genetic variance is the same. This reinforces the ideas that demography and species' details matter for this subject. The idea that demography is important for this system is not new, as other studies show that large population numbers of growth rates can be important for avoiding extinction and enabling evolutionary rescue (Burger & Lynch 1995; Carlson et al. 2014; Bay *et al.* 2017; Bell 2017). Density dependence is also important for adaptation, as alleviation of competition can be important for populations on low abundances (Carlson *et al.* 2014), although current theory is inconclusive on this effect on the system (Bell 2017). A mechanistic approach on density-dependent regulation, as performed in this work by explicitly accounting for resources, could be useful for advancing on that discussion.

We used DEB theory to generate random species with different emergent body sizes, and this allowed us to a wider look on the possibilities for different species without losses in detail of individual processes. All species we simulated had the same reaction norms between temperature and energetic expenditures. The capacity to adapt to novel environments was different, depending on the genetic variance and the species' body size. By those results, the model qualitatively agrees to the classical and trusted models of quantitative genetics and evolutionary rescue (Burger & Lynch 1995; Chevin *et al.* 2010; Bay *et al.* 2017). We found that species with intermediary body sizes should be the ones that adapt faster. This might be related to the higher reproductive potentials of species with intermediary boy sizes, as shows in chapter 2, and as has also been proposed in the literature (Bay *et al.* 2017). Generation time is also predicted to affect eco-evolutionary dynamics, and further exploration on this feature also might be interesting (Carlson *et al.* 2014). Those results also can be related to how temperature varies in time (Holt 2004), but additional investigation is needed on that topic.

Some of the simulated populations fixed their genes to newer environments, depleting genetic variance, but some of them still had genetic variability after 100 years, even in fixed temperature scenarios. This might be discordant from other results on the literature and to the classical view that stabilizing selection depletes genetic variation (Bürger & Ghnelfarb 1999). Our model did not incorporate some factors that can maintain variation in stabilizing selection (gene flow, frequency-dependent selection), and we cannot attribute this result to the one we incorporated (temporal variability in temperature) because the pattern also occurred in fixed temperature scenarios. Further investigation should clarify why this effect emerges from the system, as it could be an effect of the genetic architecture and the effect sizes we assumed. The model showed that the speed of adaptation was lower in most extreme temperature scenarios. Models that examine gradual change in temperature led to the contrary, in which higher environmental changes led to faster adaptation and environmental tracking (Pease *et al.* 1989; Kingsolver & Gomulkiewicz 2003; Kingsolver *et al.* 2004), but our results agree to models that incorporate abrupt changes in evolutionary rescue scenarios (Bay et al. 2017). It is possible that this is caused by demographic factors, as more extreme temperatures probably lead to a higher reduction of population numbers in the beginning of the runs, and we would need a deeper analysis on results to explore that emergence. We still need to evaluate how this model would predict evolution on a gradually changing environment in order to properly compare our results to some studies in the literature.

Our results show how intra-specific variability coupled to heritability can have effects on population dynamics. Overall, adaptation led to increases of population numbers, although the magnitude of this effect showed complicated patterns. The model suggests that adaptation can lead to novel aspects of population dynamics, affecting population fluctuation and means and variance in novel combinations. We believe that further investigations of more detailed descriptions of populations dynamics could be interesting, just as observing changes on other descriptors of the populations (voltinism, distributions of body sizes, etc.). Also, temporal variability on temperature diminished the positive effects of adaptation in our system. This result is very relevant, as climate change is predicted to also impact variation and temperature extremes (Seneviratne *et al.* 2014). There was a small but significant number of cases in which species seem to have maladapted, and also that adapted species displayed reductions in individual number. One of the most interesting emergencies from chapter 2, which depicts the system of the model we used as basis, was that population abundance can be suboptimal in relation to optimal temperature. That finding can be important for the results we show here, as we should investigate in further explorations of this model.

An interesting result was found regarding species' extinction. Higher magnitudes of temperature change (the +6 and -8 scenarios) predictably led to higher changes of extinctions, on wider ranges of species' body sizes. In fixed temperature scenarios, smaller species were the ones with larger chances for extinction, as long as in fluctuating scenarios larger species were more probable to go extinct. The pattern of the extinction probability related to body sizes was much weaker in fluctuating temperatures, suggesting fluctuations affect all species, not only larger ones. Fixed temperature scenarios do not happen in nature, so the importance of those scenarios in this simulation have a more theoretical foundation. We could argue that the highest extinction probability for smaller species could be related to their lower reproductive capacity, that can hamper recovery from abrupt population declines at the beginning of the simulations. However, we could not explain why big species that also have low reproductive outputs (and larger generation times) could "escape" from that process. A possibility for the pattern can be understood regarding generation time. As the generation times of smaller species is very small, it is possible that some of their genetic variation was already depleted before the first annual fluctuations of temperature. This would mean the species adapt fast enough to a range of temperatures that is not the one fully present on that environment, and this rationale could be compared to the concept of evolutionary traps (Robertson *et al.* 2013). Some extinctions of smaller species also happened in the fixed scenario of no temperature change, and this suggests that those extinctions might also be explained by the individual variability (as those species were viable in that same scenario from the second chapter, from which the only difference is the individual variability). Predicting higher danger for smaller species is very meaningful, and this is an important result that demands further exploration.

The populational IBM used as basis was developed to overcome some theoretical limitations of population ecology. By the same rationale, its' application to this specific problem also displays advances. It was already acknowledged that the need of prediction for population genetics under multiple varying loci are a field in which individual-based models could help (Judson 1994), and our work helps filling that gap. We developed the model based on sub-models that can be used and enhanced to apply for a variety of species, without losing track of realism, and that have a high potential to generate standardization of sub-models of individual-based models. DEB theory, the theoretical body from which we borrowed some assumptions for the energetic dynamics od he models' individuals, is a highly validated field both in empirical assessments (Kooijman *et al.* 2008; van der Meer *et al.* 2014; Augustine & Kooijman 2019) and theoretical approaches (Einarsson *et al.* 2011; Monaco *et al.* 2014; Agüera *et al.* 2017). We believe that questioning local adaptation and evolutionary rescue integrated to DEB theory helps both in integration with empirical efforts and in communication between different models and theoretical approaches. Our model also runs on a concrete time scale, and therefore should also be straightforward for validation purposes (Uchmánski & Grimm 1996; Lavergne *et al.* 2010). Explicitly accounting for gens and genetic architecture through their individual effects might also be important for validation, especially due to advances on genomics related to finding genes responsible for environmental relationships (De Jong 1990; Tiffin & Ross-Ibarra 2014; Chen *et al.* 2018).

The results we show in this chapter are initial explorations of the system. Some simplifications could be changed in order to make other relevant predictions, and parts of the model could be enhanced. At first, we could analyze how species with different sensitivities could respond differently to the change. From thermal ecology, we know that there are different possibilities for constraints on thermal preference (Huey & Kingsolver 1989; Angilletta *et al.* 2003; Gvoždík & Van Damme 2008), and they might have consequences and lead to novel patterns of adaptation (Huey & Kingsolver 1989; Gabriel & Lynch 1992; Gilchrist 1995). Optimality theory (Lynch & Gabriel 1987; Gilchrist 1995) shows that the form of reaction norms is important for organisms' fitness under fluctuating environmental regimes, and advancing on exploring this feature with the model developed here could be very interesting. The model is also open to simulate the effects of different scenarios of resource abundance. Species are overall threatened not only to environmental change, but to other anthropogenic impacts like habitat loss or pollutants (Newbold *et al.* 2015; Trathan *et al.* 2015), which may be interpreted and simulated as changes in resource levels and demographic parameters. A complete understanding of the responses of species to climate change must incorporate different pressures on the populations, and our framework could help on theorizing about their effects.

The framework also could have been observed by different ways. It is a stochastic model, so we could generate better predictions on extinction by more replications in the meta-modelling design. Also, we could have analyzed changes on other aspects of the populations, for example body sizes and changes in demographic rates (e.g., reproductive rates and death rates). We evaluate that running a lower number of species, under a wider variety of scenarios could have interesting results, as it would enable analysis on wider ranges of temperature regimes (both in magnitude of temperature change and variation).

In real world, local adaptation also can depend on other features not included in this model, as for example, phenotypic plasticity (Thompson 1991; Fierst 2011; Wund 2012) and behaviors like thermoregulation (Boyles *et al.* 2011). It is also proposed that this adaptation may interact with other important traits, related to life history, for example (Reed *et al.* 2011; Dytham *et al.* 2014). There is still debate on how phenotypic plasticity may interact with adaptation, as it may be adaptive (by exposing species to novel environments in which selection might occur afterwards) or not (by countering the relative fitness benefits of adapted organisms) (Ghalambor *et al.* 2007). Also, integration between thermal preference and thermal sensitivity theories are also needed to understand how they can interact and lead to optimal strategies for facing different environments (Angilletta *et al.* 2002, 2006).

The most interesting addition to this model would probably be of a spatial structure, allowing for migration and gene flow. From a theoretical perspective, intra-specific variability and local adaptation in traits also matter for higher levels of biological organization, for example the dynamics of species' ranges (Kirkpatrick & Barton 1997; Sexton *et al.* 2009). There is still doubt on the effects of gene flow on local adaptation, and this effect is crucial for understanding ranges. Gene flow from central adapted populations might hamper adaptation on edges through swamping of maladaptive genes (Kirkpatrick & Barton 1997), but it also may save species on sink environments from losing genetic diversity through genetic drift (Alleaume-Benharira *et al.* 2006). Until the moment, the dynamics of species' ranges and the adaptation potential within them are highly debated, as a consensus for what limits species' ranges is lacking (Bridle *et al.* 2010; Polechová 2018). Overall, models theorizing on species ranges follow some assumptions (Sexton *et al.* 2009 for a review), like simple relationships between individual fitness and demography or simple quantitative traits, and they often do not account for factors that can limit genetic diversity and other important drivers of the relationship between demography and the environment. Some individual-based models have helped advancing on that field, incorporating factors like genetic drift (Alleaume-

Benharira *et al.* 2006), temporal variability (Holt *et al.* 2004), and better depictions of demographic factors (Atkins & Travis 2010; Bridle *et al.* 2010), but we state that a more complete usage of what IBMs provide would be interesting for further advances on this field.

Conclusions

The most important conceptual feature of this framework is how evolution occurs in an emergent fashion, not needing some assumptions on forms and intensities of selection pressure as in the quantitative genetics' approaches. We were able to simulate fast adaptation as an emergent feature, given that the basic and classical premises for selection are present in the system. We produced patterns highly concordant to withstanding theory, and those patterns are resultant from combinations of processes on lower levels of biological organization. With this model, we predicted how different species might respond to abrupt changes in temperature regimes, and how those responses are related to the population dynamics generated by the model. We reinforce the view that ecological and evolutionary time scales might not be so discrepant as early thought, and that it is possible to build mechanistic models with a relevant amount of detail that are also general enough to be important for theory. The subject we explored here is of high importance for theories on higher levels of organization (e.g., species' ranges) and also for forecasts of practical questions (how species will respond to climate change). We believe that future work on this model, by adopting higher levels of detail on different aspects of its' design can be very useful for advancing on ecological theory.

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CONCLUSÃO GERAL

Nesta contribuição, investigamos como mudanças em regimes de temperatura podem afetar sistemas ecológicos e biológicos. Investigações empíricas sobre os efeitos da temperatura em organismos e espécies tem uma longa história, e nos levaram a importantes conhecimentos. No momento, uma porção significativa dos efeitos da temperatura são bem entendidos e estudados, mas ainda precisamos avançar especialmente sobre o efeito da temperatura em escalas organizacionais superiores aos indivíduos (em escalas evolutivas, geográficas, populacionais). Aqui, desenvolvemos um modelo populacional para os efeitos da temperatura em populações, levando em consideração detalhes da história de vida dos organismos e mecanismos para a regulação denso-dependente das espécies. Usamos a teoria DEB como uma ferramenta para gerar espécies virtuais, criando assim um modelo com quantidade relevante de detalhes e realismo que não perde em capacidade de generalização. O conceito mais importante explorado nesta tese é o da emergência. Nós simulamos sistemas complexos de maneira realista, com importantes concordâncias e discordâncias em relação a atual teoria, através do escalonamento de processos do nível do indivíduo para níveis de organização superiores. Assim, temos importantes conclusões, como as possibilidades de que abundância populacional das espécies pode ser sub ótima em relação à temperatura, que espécies de tamanhos intermediários podem ter maior potencial para adaptação rápida e que o escalonamento direto do fitness dos indivíduos para o nível populacional pode não ser algo adequado. Nós acreditamos que melhorias e mudanças em sub modelos e pressupostos do nosso trabalho podem levar a avanços teóricos em várias questões relacionadas a como a temperatura afeta os sistemas biológicos. Estudos futuros, incorporando processos como termorregulação e plasticidade fenotípica, ou incorporando mais realismo na parametrização e construção das espécies podem ser muito interessantes para gerar avanços e para um melhor aproveitamento das funcionalidades que modelos baseados em indivíduos proporcionam.

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